# Linking habitat to spatial and temporal variability in individual energetic condition: towards assessing freshwater habitat quality for Coho salmon (*Oncorhynchus kisutch*)

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#### Abstract

Spatial and temporal variation in habitat can impact individual fish energetics by influencing growth, energy storage and survival, ultimately shaping population dynamics. However, few studies have explicitly linked habitat variation to individual energetic condition. I investigated the influence of freshwater habitat characteristics on juvenile coho salmon (*Oncorhynchus kisutch*) condition, using physiological (*e.g.* lipid concentration, energy density) and morphological (relative condition factor) metrics across 13 streams in interior British Columbia. I then examined seasonal changes in condition metrics (July 2022 to April 2023) in three focal streams. Among sites, I found that different habitat characteristics best explained each condition metric. Particularly, lower water temperature was correlated with higher percent lipid. Juvenile coho salmon energetic condition declined over summer (July-September) and again over winter (September-April), indicating seasonal variation in fish condition. Collectively, this research reveals the potential for warm temperatures in these food-limited systems to limit juvenile salmon energetics. My findings are a step towards the application of juvenile salmon energetic condition as an indicator of habitat to inform conservation.

Keywords: condition; energetics; juvenile salmon; lipid; physiology; Thompson River

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iv

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# **Table of Contents**

Decla	ration of	Committee	. ii
Abstr	act		iii
Ackn	owledger	nents	iv
Table	of Conte	ents	vi
List o	f Tables		' <b>iii</b>
List o	f Figures	3	ix
1.	Introdu	ction	.1
2	Method	le	9
2. Fynerimental Design			. /
2.1.	2 1 1	Study Area	. 9
	2.1.1.	Focal Species	. ) 11
	2.1.2.	Fish Sampling	12
	2.1.3.	Physiology Sample Collection	12
		Fish Densities	13
2.2.	Habitat	Variables	14
	2.2.1.	Water Temperature	14
	2.2.2.	Nutrients	14
	2.2.3.	Physical Habitat Characteristics	15
	2.2.4.	Seasonality	15
2.3.	Physiol	ogical Analyses	16
	2.3.1.	Lipid Extraction	16
	2.3.2.	Moisture, Protein, and Energy Density	17
	2.3.3.	Relative condition factor $(K_n)$	18
2.4.	Data An	alyses	19
	2.4.1.	Among-Site Variation in Energetic Condition	19
		Model Description	19
		Model Selection and Averaging	20
		Evaluation of Condition Metrics	21
	2.4.2.	Seasonal Variation in Energetic Condition	22
		Model Description	22
3	Results		24
3.1	Among-	Site Variation in Energetic Condition	24 74
5.1.	3.1.1	Individual fish size and condition metrics	24
	312	Linking fish energetic condition to habitat variables	27
	5.1.2.	Juvenile Percent Linid	27
		Relative condition factor (K <sub>n</sub> )	27
		Energy Density	28

	3.1.3.	Comparison of condition metrics	30	
3.2.	2. Seasonal Variation in Energetic Condition			
		Percent lipid	33	
		Percent protein	34	
		Relative condition factor (K <sub>n</sub> )	35	
		Energy Density	35	
4.	Discuss	ion	36	
4.1.	Overvie	w of key findings	36	
4.2.	Linking	fish energetic condition with among-site habitat variation	37	
4.3.	Linking fish energetic condition with seasonal habitat variation			
4.4.	Integrat	ion of condition metrics	44	
4.5.	Limitati	ons and future directions	47	
4.6.	Manage	ment implications	48	
4.7.	Conclus	ion	51	
Refer	ences		52	
Appe	ndix. Sı	applemental Tables and Figures	69	
Hiera	rchical B	ayesian Closed Mark-recapture Overview	69	
Amor	ng-Site V	ariation	74	
Seaso	nal Varia	ation	80	

# List of Tables

Table 1.1.	Hypotheses for the potential influence of fish metrics and among-site and temporal variation in habitat and environmental variables on the salmon condition metrics percent lipid, energy density (ED) and relative condition factor ( $K_n$ ). Direction of predicted effect is noted (positive or negative) 7
Table 3.1.	Top models (selected as the least complex model within $\Delta AICc < 2$ ) from modelling juvenile condition using three metrics. Aikaike information criterion (AIC) corrected for small sample size (AICc) was used to determine top model. Note mass, age and mass:age interaction were included in all models during selection process. All models contain a site- level intercept informed by site-level habitat variables
Table 3.2.	Condition metric measurements with standard deviation (percent lipid and protein, relative condition factor ( $K_n$ ), and energy density) across three sites between the months of July to September 2022, and April 2023, with standard deviation. The samples used for lipid analysis and $K_n$ are noted by $n$ , while the samples that were also used for energy density analysis are noted in brackets

# List of Figures

Figure 1.1.	Diagram explaining the effect of biotic and abiotic factors on individual fish energy intake and the allocation of surplus energy. The combination of biological and habitat variables (biotic and abiotic) influence both the energy available for intake and the energetic costs, determining an individual's metabolic requirements and energetic allocation strategies for surplus energy. Density acts as a mediator for the other variables, influencing the absolute energy intake for a given individual. Pink boxes represent metabolic maintenance costs required for survival, while green indicates positive intake of energy that can be allocated to growth or storage. Condition metrics used in this study to identify energetic condition and energetic allocation are indicated in the dark green boxes 6
Figure 2.1.	Study site locations in tributaries along the North Thompson River in British Columbia. Each site is numbered and has a unique colour that is shared across all figures. Study sites are ordered North to South: 1) Albreda, 2) Cook, 3) Cedar, 4) TumTum, 5) Shannon, 6) Reg Christie, 7) Chuck, 8) Lemieux, 9) Fennell, 10) Haggard, 11) Louis, 12) FishTrap, 13) Jamieson
Figure 2.2.	Representation of the habitat variation in sites used in this study. Sites shown are A) Cedar, B) Tum Tum and C) Reg Christie
Figure 3.1.	The age-specific relationships between each condition metric and the significant variables from the hierarchical model. The regression line and 95% confidence area of the model-averaged coefficients are shown for each condition metric: Top Row: Percent lipid and A) Mass, B) Large Wood (LW), C) Accumulated Thermal Units (ATUs), Middle Row: Le Cren's relative condition factor ( $K_n$ ) and D) Mass, E) LW, F) Gradient, and Bottom Row: Energy Density (ED) and H) Mass, and I) Total Phosphorus. Triangles, solid regression line and darker 95% confidence region shading represent the Age 1+ fish, while circles, dashed regression line and lighter 95% confidence region shading represent Age 0+ fish 26
Figure 3.2.	Standardized model-averaged coefficients (points) with 95% conditional confidence intervals (lines) for condition metrics A) percent lipid, B) Le Cren's relative condition factor ( $K_n$ ), and C) energy density (ED). Explanatory variables are presented for each response variable in decreasing order of their Relative Variable Importance (RVI) value (indicated on right). An asterisk (*) beside the RVI value indicates the variable was fixed to be included in all models (age, mass and the agemass interaction). 29
Figure 3.3.	Percent lipid, percent protein, Le Cren's relative condition factor ( $K_n$ ) and Energy Density (ED) coefficients across months for the Cedar, Reg Christie and Tum Tum sites, with 95% confidence intervals. The coefficients were calculated for each site using a base linear regression model of condition with predictors mass, month and a month-mass

### 1. Introduction

The interaction between an individual fish and their habitat can affect physiology, behaviour, life-history and overall condition (Chaparro-Pedraza & de Roos, 2019; Gaillard et al., 2010; Horodysky et al., 2015; Patterson et al., 2016). Overall condition can be used to define a suite of indices (often proxies of energy reserves) that may be predictive of an individual's survival (Bolger & Connolly, 1989; Stevenson & Woods, 2006; Wikelski & Cooke, 2006). The influence of habitat on overall condition can therefore affect an individual's odds of survival, possibly scaling into population-level consequences (Cooke et al., 2013; Mallett et al., 2024). Habitats with more resources and lower energetic costs (*i.e.* higher net energy availability) could lead to increased population-level energetic intake and an increase in biomass (Brownscombe et al., 2022). Density dependent processes modulate energy intake at the individual level, influencing how much energy is available to each fish (Matte et al., 2020, 2021). Following essential metabolic processes, individual fish allocate surplus energy to growth and/or energy storage (Biro et al., 2006; Brett et al., 1969; Post & Parkinson, 2001). An individual's energetic condition may therefore reflect the combined effects of physical habitat and fundamental biological processes on individual energetics, and subsequently survival (Figure 1.1) (Brownscombe et al., 2022; Tomlinson et al., 2014).

Physiological metrics (assessing cellular, organ and organismal function) can provide a mechanistic understanding of how individual fish energetic condition responds to current and future habitat variation. Measuring individual energetic condition in a population is increasingly recognized as a valuable aspect of conservation management for many species, driving expansion in the field of conservation physiology (Cooke et al., 2013; Wikelski & Cooke, 2006). Understanding individual-level responses to habitat variation clarifies the mechanistic pathways between habitat and population changes, improving conservation management models for predicting population-level outcomes (Horodysky et al., 2015; Mallett et al., 2024; Patterson et al., 2016; Stevenson & Woods, 2006). Pacific salmon *(Oncorhynchus spp.)* are one group of species sensitive to changes in their freshwater rearing habitat, with variation in energetic condition across habitats

and among seasons linked to survival (Beechie & Sibley, 1997; Bisson et al., 2009; Gallagher et al., 2022; Stevenson & Woods, 2006). However, research quantifying the linkages between salmon energetic condition and habitat remains limited (Brownscombe et al., 2022; Cooke et al., 2012; Patterson et al., 2016).

The utility of population density, morphometric and physiological metrics in conservation can depend on the species, habitat, and level of resolution required (Hayes et al., 2009; Hurst & Conover, 2003; Schloesser & Fabrizio, 2017). Density is frequently used to represent population-level overall condition, as a broad assessment of the relationship between organisms and habitat (Van Horne, 1983). Comparatively, individual condition metrics (morphometric and physiological) may show a measurable response to habitat variation within a shorter timeframe. For example, Polivka (2020) observed no change in Pacific salmon sub-yearling densities but noted significant improvements in size and morphometric condition at restoration sites, suggesting a response undetected by density measurements. Thus, compared to population-level or morphometric measurements (*e.g.* body shape or size) (Currens et al., 1989), physiological metrics may be more reflective of fish energetic condition (Brosset et al., 2023; Mallett et al., 2024).

Morphometric measurements can be useful indices of individual overall condition but may not capture key physiological processes directly related to energy reserves (Brosset et al., 2023; Schloesser & Fabrizio, 2017; Wilson et al., 2021). In experimental swim trials of sockeye salmon smolts, Wilson et al. (2021) found physiological metrics of energetic condition (protein content and energy density) best predicted survival, but a morphometric measurement (condition factor) was the best predictor for swim performance. Trudel et al. (2005) found that Fulton's condition factor or length measurements were not representative of direct measurements of energy density in juvenile salmon. These findings suggest that morphometric measurements may reflect traits other than energy reserves that are important for survival. Therefore, using physiological metrics of energetic condition could improve understanding of how habitat changes (*e.g.*, degradation or restoration) specifically impact fish energetics.

Using tissue biochemical indices (e.g. whole-body lipid and protein, and energy density) to measure energetic condition allows for comparison of relative growth and energy storage across space and time. As the main energetic constituents of fish, lipid and protein content can indicate salmon energetic condition (Næsje et al., 2006; Weber et al., 2003) and even predict survival (Simpkins et al., 2003; Wilson et al., 2021). Energy available in a habitat influences the energetic condition of individual juvenile salmon across seasons and into future life stages (Birnie-Gauvin et al., 2021; Biro et al., 2021; Rosenfeld et al., 2020). Measuring energy storage reflects an individual's energy intake, potentially indicating the habitat's energetic availability. Energy storage also offers insight into a fish's ability to endure future periods of food scarcity or environmental stress, making it a more integrative predictor of survival. For instance, during migration to the ocean, Hanson et al. (2012) found juvenile Chinook salmon temporarily using offchannel habitats had higher energetic condition compared to those in mainstem habitats, suggesting higher energy reserves to compensate for the energetic costs of migration. Measuring fish energetic condition could be especially informative in environments with fluctuations in energy availability, either due to seasonal shifts or habitat degradation.

Individual juvenile salmon use most energy for metabolism, and must balance the trade-offs between allocating surplus energy towards either somatic growth or lipoprotein storage (Brett et al., 1969; Martin et al., 2017; Metcalfe et al., 2002; Mogensen & Post, 2012; Rosenfeld et al., 2020) (Figure 1.1). Habitat influences the amount of surplus energy available, and environmental demands shape energy allocation strategies (Hurst & Conover, 2003; Post & Parkinson, 2001). Variation in habitat factors can affect both energetic availability and costs (Beerens et al., 2015), resulting in shifts in energy use towards storage or growth based on survival requirements (Birnie-Gauvin et al., 2021; Biro et al., 2004; Hurst, 2007; Mogensen & Post, 2012).

Temporal variation in habitats may drive shifts in energy allocation. For instance, to prepare for energy-deficit periods like overwintering, juvenile salmon may adjust energy allocation to balance predation and starvation risks (Biro et al., 2005). Fish adjust their energy allocation based on environmental factors (e.g., duration of deficit) and individual traits (e.g., mass-specific metabolic rates, genetics) (Biro et al., 2004; Hurst,

2007; Mogensen & Post, 2012). During the growing season, predation risk may drive energy allocation towards growth to reduce predator vulnerability (Hurst & Conover, 2003; Metcalfe et al., 2002), while in winter, the risk of starvation increases as lipid reserves are depleted for metabolism (Biro et al., 2006; Giacomini & Shuter, 2013; Post & Parkinson, 2001). Prioritizing high energy density lipid stores before periods of energy scarcity is a common strategy seen in temperate fish (Hurst, 2007). Understanding these allocation strategies and their temporal variability allows for interpretation of energetic condition in relation to both temporal and spatial habitat variation.

A suite of key habitat features can affect juvenile salmon energetic condition, often through complex interactions (Figure 1.1). Individual energy storage has been connected to abiotic and biotic habitat structure (*e.g.* food availability, temperature, nutrients, water chemistry and stream hydrology) (Bisson et al., 2009; Railsback, 2022; Roni & Quinn, 2001; Volkoff & Rønnestad, 2020), increased latitudes and elevation , and biological factors like body size (Berg et al., 2011; Finstad et al., 2009; Post & Parkinson, 2001) and life history strategy (*e.g.* migration timing) (Morgan et al., 2002). Changes in physical habitat structure (*e.g.* hydraulic habitat composition, large wood, and substrate) can influence juvenile salmon energetics by changing access to predator refuge and food sources (Bisson et al., 1988; Ebersole et al., 2006; Naman et al., 2018; Roni & Quinn, 2001; Rosenfeld et al., 2005).

Stream temperature is a key driver of size and condition-dependent processes at early life stages (Ebersole et al., 2006; Volkoff & Rønnestad, 2020). Generally, peak juvenile salmonid growth rates and condition occur in cool thermal regimes (Reiser & Bjornn, 1979). Higher rearing temperatures may result in decreased juvenile salmon overall condition, evidenced by earlier migration and smaller sizes (Braun et al., 2013), decreased growth (Neuheimer et al., 2011), predation vulnerability, swimming performance (McInturf et al., 2022) and lower lipid values (Feldhaus et al., 2010; McMillan et al., 2012). Temperature also interacts with ration (food availability) by influencing energetic requirements, food-seeking behaviour, and even digestion and processing (Brett et al., 1969; Iino et al., 2022; Kaylor et al., 2019; Lusardi et al., 2020; Railsback, 2022). As metabolic rates rise with temperature, fish must increase food intake to maintain their standard metabolic rate, further linking temperature to energetic condition (Brett et al., 1969; Volkoff & Rønnestad, 2020). Despite numerous studies on salmon habitat, few have quantified how temporal and spatial variation in specific habitat features can influence juvenile salmon energetic condition.

Here I examined how variation in freshwater habitat in interior British Columbia streams influences juvenile coho salmon (Oncorhynchus kisutch) energetic condition. I aimed to (1) improve understanding of key drivers of spatial and temporal differences in energetic condition and (2) assess use of physiological metrics as potential tools for evaluating habitat. I assessed these objectives in two parts: an among-site study, which investigated how habitat differences across sites affected fish condition, and a temporal study, which measured how condition changed across months to capture seasonal variation. Across these two studies, I evaluate juvenile coho salmon individual energetic condition with three metrics: (1) Whole-body lipid percent (lipid), (2) Le Cren's relative condition factor  $(K_n)$ , and (3) Energy Density (ED). A fourth metric, whole-body protein percent was used only in the temporal study in conjunction with lipid to examine changes in energy allocation across seasons. I hypothesize that individual juvenile coho energetic condition will (1) differ across habitats in response to variation in stream habitat variables, and (2) show seasonal variation within a habitat due to changes in abiotic and biotic habitat variables over time (Table 1.1). I further predict that lipid and ED will show higher sensitivity to changes in habitat and more seasonal variation than  $K_n$ , but the three metrics will show similar relationships to among-site variation in habitat variables (Trudel et al., 2005). Understanding the mechanistic relationships between biological responses and habitat may help predict the impacts of current and future habitat variation on salmon energetic condition and energetic allocation strategies (Aldridge & Boyce, 2008; Mogensen & Post, 2012; Post & Parkinson, 2001).



Figure 1.1. Diagram explaining the effect of biotic and abiotic factors on individual fish energy intake and the allocation of surplus energy. The combination of biological and habitat variables (biotic and abiotic) influence both the energy available for intake and the energetic costs, determining an individual's metabolic requirements and energetic allocation strategies for surplus energy. Density acts as a mediator for the other variables, influencing the absolute energy intake for a given individual. Pink boxes represent metabolic maintenance costs required for survival, while green indicates positive intake of energy that can be allocated to growth or storage. Condition metrics used in this study to identify energetic condition and energetic allocation are indicated in the dark green boxes.

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Response Variable	Hypothesized impact on salmon condition	Direction	Measured metric	References
		Fish Metrics		
Fish Density	Given average habitat quality, increased fish density will decrease individual fish energetic condition	Negative	Estimated juvenile coho density (fish/m <sup>2</sup> )	(Grossman & Simon, 2020; Hasegawa et al., 2024; Matte et al., 2021; Rosenfeld et al., 2005; Utz & Hartman, 2009; Vincenzi et al., 2012)
Age	Energetic condition is higher for an Age 1+ fish compared to an Age 0+ fish of the same mass.	Positive	Fish age	(Biro et al., 2005; Ebersole et al., 2006; Jonsson & Jonsson, 2003; Post & Parkinson, 2001)
Size	A positive allometric relationship between size (length or mass) and condition, with highest condition in larger juveniles.	Positive	Whole body mass (g)	(Biro et al., 2004, 2005; Hurst & Conover, 2003; Post & Parkinson, 2001)
	Envir	onmental Varial	bles	
Season	Season can affect habitat variables, in turn affecting juvenile energetic condition (especially through temperature). Temporal variability in energy storage is also expected in response to seasonality (preparation for overwintering energetic storage).	Positive (April- September), negative (September - April)	Month (spring (April), summer (July/ August), or fall (September)	(Biro et al., 2021; Cleary et al., 2012; Hurst & Conover, 2003; Mogensen & Post, 2012; Post & Parkinson, 2001; Spangenberg et al., 2023)
		Higher across- season sensitivity in lipid and ED,		

Response Variable	Hypothesized impact on salmon condition	Direction	Measured metric	References
Geospatial location	Location influences energetic availability and allocation strategies, likely encompassing environmental gradients of other habitat variables. Higher elevations and latitudes will lead to cumulatively longer periods of energetic taxation ( <i>i.e.</i> overwintering). Fish at lower latitudes and elevation sites will accumulate relatively less energy stores, and show lower seasonal variation, due to differing overwinter energetic storage requirements to stay above the minimum energetic survival threshold.	Positive	Latitude and Elevation	(Berg et al., 2011; Biro et al., 2004; Gallagher et al., 2022; Parra et al., 2009; Yamahira & Conover, 2002)
Water temperature	Increased temperatures will decrease energetic condition by increasing metabolic costs to individual fish.	Negative	Accumulated thermal units (ATUs)	(Araújo et al., 2023; Armstrong et al., 2021; Lusardi et al., 2020; Volkoff & Rønnestad, 2020)
Habitat Complexity	Increased habitat complexity will provide higher quality habitat, potentially through improved food availability and energetic refuge.	Positive	LW pieces by total area (m <sup>-2</sup> ), pool:riffle ratio	(Bisson et al., 1988; Ebersole et al., 2009; Fausch & Northcote, 1992; Jorgensen et al., 2021; Mellina & Hinch, 2009)
Gradient	Juvenile coho salmon preferentially select low- gradient habitat, therefore this habitat likely corresponds to increased condition due to improved energetic refuge and potentially food resources.	Negative	Gradient (percentage)	(Beechie & Sibley, 1997; Bryant et al., 2004)
Nutrients	Higher nutrients are indicative of energy available in the system for primary and secondary productivity, leading to increased energy available for salmon consumption. Higher energy intake will lead to increased condition.	Positive	Dissolved Total Phosphorus (µg/L)	(Kiffney et al., 2014; Lusardi et al., 2020; Naman et al., 2022)

### 2. Methods

### 2.1. Experimental Design

#### 2.1.1. Study Area

I studied 13 small coho salmon streams (referred to as study sites throughout) in the North Thompson watershed (Figure 2.1) of British Columbia, Canada. This is a snowmelt-dominated watershed. Small streams experience high spring flows from snowmelt (freshet), low flows during dry, hot summer and autumn conditions, and dry, cold winters as precipitation accumulates as snow (Déry et al., 2012). Originating from the Thompson Glacier in the Cariboo Mountains, the North Thompson River flows towards Kamloops, joining the South Thompson River to become the Thompson River, the largest tributary of the Fraser River. The North Thompson watershed features diverse physical stream habitat and a climate gradient from northern high-elevation streams with long, cold winters to southern low-elevation streams with warmer summers and winters (Figure 2.2). The watershed has notable anthropogenic impacts, including historical and current logging activity, linear development, and residential and agricultural land use in the south (Bradford & Irvine, 2000).



Figure 2.1. Study site locations in tributaries along the North Thompson River in British Columbia. Each site is numbered and has a unique colour that is shared across all figures. Study sites are ordered North to South: 1) Albreda, 2) Cook, 3) Cedar, 4) TumTum, 5) Shannon, 6) Reg Christie, 7) Chuck, 8) Lemieux, 9) Fennell, 10) Haggard, 11) Louis, 12) FishTrap, 13) Jamieson.

Study sites were selected based on ease of access, the presence of juvenile coho salmon, and their diverse habitat and environmental characteristics (Table A.3) (Cunningham et al., 2023). Sites were divided into reaches of specific lengths. Water temperature and physical habitat data for reaches (gradient, water chemistry, large wood (LW), wetted width, etc.) were collected from July to August in 2019 and 2020 (Cunningham et al., 2023), and from April to October in 2021-2023. Juvenile coho salmon density was measured at each sampling event.



Figure 2.2. Representation of the habitat variation in sites used in this study. Sites shown are A) Cedar, B) Tum Tum and C) Reg Christie.

#### 2.1.2. Focal Species

This study focused on juvenile coho salmon from the North Thompson (NT) Conservation Unit (Arbeider et al., 2020); one of five population complexes included in the Interior Fraser River Coho (IFC) salmon Designatable Unit (COSEWIC, 2016). The IFC has been designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Threatened due to marine survival declines and threats to their freshwater habitat like drought, increased water temperatures and urbanization (Arbeider et al., 2020; COSEWIC, 2016). The IFC encompasses all coho populations that spawn upriver of Hells Gate in the Fraser River watershed in British Columbia, and are genetically, morphologically and behaviorally distinct from other populations in the lower Fraser River and coastal populations (Arbeider et al., 2020). Coho fry emerge in the spring between March and July after adults spawn in the prior fall and early winter. Juvenile coho then spend one to two years in freshwater systems, spending most of their time rearing in natal streams, wetlands, side channels, and the mainstem before migrating to the ocean as smolts (Arbeider et al., 2020). Most IFC typically spend eighteen months in the ocean before returning to freshwater to spawn (Groot & Margolis, 1991).

#### 2.1.3. Fish Sampling

I conducted studies to explore 1) among-site variation of juvenile coho salmon energetic condition across the 13 sites, and 2) temporal variation of energetic condition across a 10-month period using a subset of sites (n=3 sites). For the among-site variation study, juvenile coho salmon were sampled once in September 2020 at all 13 sites to collect physiological samples and estimate density. Fish captured consisted of age 0+ and 1+ juvenile coho salmon. A subset of three sites was sampled in July, August, and September 2022, and again in April 2023 for my temporal variation study. Fish from Tum Tum Creek in April 2023 were not included in my study due to a fish salvage release during the time of our sampling. At each fish sampling event and site, up to 30 1/8" minnow traps (Gee traps) were distributed in typical coho habitat throughout reaches for the mark-recapture study and 10 minnow traps were placed outside of the reaches (above and below) to collect fish for physiology samples. Fork length and wet mass were measured to the nearest millimeter and 0.1 gram, respectively.

#### **Physiology Sample Collection**

Fish used for physiological assays were collected from just outside the reach used to characterize habitat and juvenile coho salmon densities at each site. Thirteen to 46 juvenile coho salmon (mass range of 0.8-16 g) were randomly sampled from minnow trap catches. These fish were euthanized with a lethal dose (100-200 ppm) of buffered MS-222 solution, measured and immediately frozen on dry ice in individual labeled bags. Upon return from each sampling trip, fish were transferred to a -80°C freezer for long-term storage. The fish are from two cohort years, divided into young-of-the-year (Age 0+) juveniles, and parr that hatched the previous year (Age 1+). Individual fish collected in 2020 were aged via visual inspection of scales (*sensu* Milner, 2023). To test the assumption that the fish sizes used for physiological assays were representative of the population, I compared the fork length distribution of fish collected for physiological analysis with that of the total catch for each site (Figure A.3). However, due to a minimum size cutoff for the physiological assay used to calculate energy density, smaller fish were underrepresented in the final analysis. See below for further information on methods of physiological analyses.

#### Fish Densities

Density can have strong impacts on intraspecific competition and habitat selection, influencing individual energy intake from the surrounding habitat and ultimately affecting individual energetic condition (Grossman & Simon, 2020). As part of another project, juvenile coho salmon densities were estimated with a closed markrecapture technique using minnow trapping and Visible Implant Elastomer tags (Northwest Marine Technologies, Shaw Island, WA) for marking. The mark-recapture sampling events took place over three days. On day one baited traps were placed into the stream reaches. On day two, captured coho were counted, measured and marked if their fork length was  $\geq$  35 mm. All fish were released back into the reaches and traps were reset with new bait. Traps were retrieved on day three, and fish counts and measurements were repeated, noting the numbers of marked and unmarked fish. Fishing time for each set was typically between 12 and 24 hours, but exact time was recorded to calculate fishing effort. Fish captured within the study reach were held in buckets with aerated water at ambient stream temperatures and anesthetized with dissolved 40-50ppm of tricaine methanesulfonate (MS-222) soluble powder (Syndel, USA) prior to handling. After taking measurements (and marking), fish were placed into aerated buckets to recover and were released randomly throughout the reach once fully recovered. The data on juvenile coho salmon abundance and densities came from the North Thompson Salmon Ecosystem Program (Braun, unpublished data) and was estimated using a hierarchical Bayesian closed mark-recapture model (Figure A.1). The key assumptions of this model were that capture probability varies between capture events, and that the probability of recapture is size independent. The model also includes covariates for capture probability (trap density) and density (pool area) used from Milner (2023) that improve the model fit. For more information about approach, see mark-recapture methods outlined in Milner (2023) and explained in the Appendix (Table A.1, Table A.2).

#### 2.2. Habitat Variables

Key elements of freshwater salmon habitat were measured in 2020 by Cunningham (2023), and data for temperature and physical nutrients were collected in 2020 and 2021.

#### 2.2.1. Water Temperature

Water temperature is a key factor influencing salmonid overall condition and life history (Brett, 1971; Volkoff & Rønnestad, 2020). Water temperatures were recorded by HOBO U20 or TidBit loggers (Onset Computer Corporation, HOBO Water Temp Pro V2, precision +/-0.2°C) hourly at each site. These loggers were either suspended in ABS stilling wells attached to large boulders, or to steel posts. During site visits, calibrated measurements from a handheld meter (YSI +/-0.3°C) were also taken to compare to logger readings and ensure differences were <0.2°C. Mean daily temperatures and mean monthly temperatures were calculated. Additionally, Accumulated Thermal Units (ATUs) were calculated by summing daily averaged temperatures for the 30-day period prior to fish sample collection at each site. Accumulated thermal units (ATUs) among sites ranged from 297 to 386°C for the 30 days prior to sampling.

#### 2.2.2. Nutrients

I used total phosphorus (TP) as a proxy of stream productivity as it has been linked to higher primary and secondary production and fish biomass (Hoyer & Canfield, 1991; Lewis & Ganshorn, 2007). Total phosphorus levels were measured either once or twice in 2021- 2022 for 12 of the 13 sites (excluding Fish Trap) (Naman, unpublished). Based on comparison across years, the relative differences among sites in TP levels remained consistent, while within-site TP changed minimally. Therefore, I used the TP value at each site from either September of 2021 or 2022, or the average if both were taken. These values were used in my among-site analysis to represent relative across-site variation in habitat productivity at 12 sites in September 2020 (Naman, unpublished). Total phosphorus (TP) ranged from 0.75 to 12.88 µg/L.

#### 2.2.3. Physical Habitat Characteristics

Habitat structural composition is important for juvenile coho salmon for energetic and predator refuges and for resource availability. Physical habitat data were taken from Cunningham (2023). Briefly, stream habitats were measured during low flow periods in 2019 and 2020 (July-August). All larger pieces of wood within the bankfull area of each channel (length >1.5 m and diameter >0.1 m) were counted and individually measured. This measurement was then transformed into a metric of LW pieces m<sup>-2</sup> by dividing the volume of LW pieces by the bankfull area to account for the varied stream sizes across sites. Macrohabitat units were classified and pool and riffle areas were measured then transformed into a proportional metric of pool to riffle ratio, by dividing the pool area by the total area (Cunningham et al., 2023). Sites varied from higher gradient with low pool to riffle ratios, to low gradient with high pool to riffle ratios (between 4.3%-0.21% gradient and 0.05-1 pool-riffle ratio). Large wood (LW) was highly variable among sites and ranged from as low as 0.02 to 1.05 pieces m<sup>-2</sup>.

#### 2.2.4. Seasonality

Stream habitat conditions change seasonally; therefore I assumed fish collected from one month experienced a different suite of habitat variables compared to fish collected from in other months. The months sampled were intended to represent different habitat conditions across seasons, primarily distinguished by temperature. Month was used as a categorical variable in my temporal analysis (see below). In freshwater systems, habitat variables that differ across seasons include the hydrological cycle (Déry et al., 2012), photoperiod (Spangenberg et al., 2023), temperature (Berg et al., 2011; Mogensen & Post, 2012), variation in primary and secondary productivity (Kiffney et al., 2014; Myrstener et al., 2021) and other biotic factors like prey availability, competitors, and predators.

#### 2.3. Physiological Analyses

I determined energetic condition of individual juveniles by measuring isolated fractions of total lipids, moisture and carbon content. Thawed wet mass, girth, and length (postorbital-hypural length or fork length) were measured for each fish prior to homogenization. Field fork length was used in the calculation of relative condition factor  $(K_n)$  as the caudal fin was damaged on some individuals during freezer storage which made fork length measurement in the laboratory not possible. Stomachs were removed, weighed, and reweighed after stomach contents were emptied. Stomach contents were preserved in ethanol for further analysis, and two fin clips from the caudal fin were taken for other assays. Whole fish (including the stomach minus their contents) were finely minced then homogenized using the Genogrinder (SPEX<sup>™</sup> SamplePrep 2010 Geno/Grinder<sup>TM</sup>). In total, 381 juvenile coho salmon from 2020 were processed for the among-site study and an additional 166 juveniles from 2022 were processed for the temporal study. For the 2020 among-site study (13 sites), lipid concentration was determined for 354 individuals, and energy density was calculated for 239 individuals using moisture and carbon concentration following the methods outlined below. For the 2022 three-site temporal study, 166 individuals were processed for lipid analysis (15-16 samples per site and month), with protein and energy density calculated for 136 individuals. Some processed samples were eliminated due to inadequate tissue volume for replicates of lipid, moisture or carbon samples, or high variance among replicates (based on a standard coefficient of variation (CV) threshold of > 20%).

#### 2.3.1. Lipid Extraction

Whole body lipid weight and total percent lipid were determined for each juvenile. Two sub-samples of  $0.2 \text{ g} \pm 0.015 \text{ g}$  of the homogenate were used for chloroform-methanol extraction adapted from Bligh and Dyer for smaller juveniles ranging from 0.76-14.88 g (Bligh & Dyer, 1959). Whole body lipid weight was determined by calculating the ratio of extracted lipid layer weight to the homogenate sub-sample, multiplied by the whole-body weight. If replicate values of lipid had high variance (CV>20%), lipid values were taken from the average of a third and fourth

replicate provided there was sufficient homogenate. Average values were then taken across all replicates. The proportion of whole-body lipid (expressed as percentage lipid of whole-body wet mass by multiplying the proportion by 100) was calculated as an average of lipid mass across all replicates (two or four) divided by the whole-body wet mass.

#### 2.3.2. Moisture, Protein, and Energy Density

Two sub-samples of homogenate, each measuring  $0.3 \text{ g} \pm 0.015 \text{ g}$  were placed into a drying oven at 80°C for a minimum of 24 hours. Moisture (percent water) was then measured by subtracting percent moisture loss (the ratio of the dehydrated sample weight to the homogenized wet sample weight multiplied by 100). The samples were then fired in a kiln at 500°C for 2.5 hours until full combustion into ash. Samples were allowed to equilibrate to room temperature in a desiccator before sample was re-weighed. The percent carbon was calculated through the ratio of ash weight to initial homogenate subsample weight. Percent of whole-body protein (P) was calculated as the percent difference from the sum of percent water (W), percent lipid (L) and percent carbon (C) following Trudel et al. (2005) using Eq. 1.

$$P = 100 - (W + L + C)$$

Eq. 1

The percent lipid and protein were then used to calculate total energy density (ED) for each juvenile coho salmon using standard conversion factors following Breck (2008) using Eq. 2:

$$ED = LD_f + PD_p$$

Eq. 2

Where ED is energy density (kJ g<sup>-1</sup> wet weight), L is the lipid fraction measured per juvenile (g g<sup>-1</sup> wet weight),  $D_f$  is the constant representing the energetic density of lipids for coho salmon (39.54 kJ g<sup>-1</sup>) (Brett & Groves, 1979; Crossin et al., 2004), P is the estimated protein fraction per juvenile (g g<sup>-1</sup> wet weight) and  $D_p$  is the constant representing the energy density of protein calculated for coho salmon (23.64 kJ  $g^{-1}$ ) (Crossin et al., 2004; Trudel et al., 2005).

#### **2.3.3.** Relative condition factor (*K<sub>n</sub>*)

Condition factor is a morphometric measurement frequently used in studies to indicate the relative condition of a fish based on length and mass. Le Cren's relative condition factor ( $K_n$ ) is weight independent, which made it a useful comparative morphometric measurement of energetic condition for this study (Le Cren, 1951). Since I calculated  $K_n$  using mark-recapture data collected in September from 2019 to 2023, a  $K_n$ value of 1 indicates that the observed weight matches the predicted weight (*i.e.*, condition) for a coho of a given length within the North Thompson population complex. I calculated  $K_n$  for each individual fish to compare to the physiological condition metrics using Eq. 3:

$$K_n = \frac{W}{a \bullet FL^b} x \ 100$$

Eq. 3

Where *W* is fish mass (wet weight in grams), and *FL* is the fork length (mm). Parameters *a* and *b* are empirically fitted constants specific for the juvenile coho salmon collected in the North Thompson watershed (Trudel et al., 2005). The constants are the slope (*b*) and intercept (*a*) from fitting a linear regression through  $log_{10}$  transformed length and mass data collected from the mark-recapture surveys at sites in the study system in September between 2019 and 2023 (Braun, unpublished). Thus, the denominator  $a \cdot FL^b$  is the derived mean weight of coho salmon among all sites sampled between 2019 and 2023. A value greater than one indicates that for an individual of size FL, the weight was higher than predicted based on the average weight from 2019 – 2023, while a value of less than one indicates a lower relative weight. The relationship obtained was Eq. 4:

$$log_{10}W = -11.20 + 2.94 log_{10}FL$$
  
 $r^2 = 0.96 \quad n = 5320 \quad S_{X,Y} = 0.1274$ 

Eq. 4

 $S_{X,Y}$  is the standard error of the residuals, *n* is the sample size, and  $r^2$  is the coefficient of determination indicating goodness of fit. This equation is valid for 0.4-26.0 g coho salmon in these systems. This index is specific to the North Thompson population, as the *a* and *b* constants may be population specific.

#### 2.4. Data Analyses

#### 2.4.1. Among-Site Variation in Energetic Condition

#### Model Description

The objective of my among-site analysis was to examine the descriptive relationships between measured habitat variables and three condition metrics (percent lipid, relative condition factor  $K_n$ , and energy density). To test the hypotheses outlined in Table 1.1, I used a hierarchical modelling approach to account for the multi-level structure of the data (individual- and site- level explanatory variables) (Brooks et al., 2024; Gelman & Hill, 2007, p. 347). Also, the hierarchical modelling approach avoided pseudoreplication, accounting for the likelihood that individuals are more likely to be similar within a site than among sites (*e.g.* genetic similarities) (Xuereb et al., 2022). I hypothesized that fish size is an important predictor of condition and energetic allocation. Additionally, to address differences observed in the mass – condition relationship across ages, I included an age-mass interaction in the model for each condition metric. I used a beta regression for lipid and logit-transformed the data to improve normality and homogeneity of variance (Douma & Weedon, 2019; Geissinger et al., 2022). I used a Gaussian distribution in the global models for  $K_n$  and energy density.

The Gaussian global model structure describing condition metrics is as follows:

$$Y_{i} = (\alpha + \mu_{j[i]}) + \beta_{1}Mass_{i} + \beta_{2}Age_{i} + \beta_{3}(Mass_{i} * Age_{i}) + \varepsilon_{i}, \qquad \varepsilon_{i} \sim N(0, \sigma_{Y}^{2})$$
$$\mu_{j} = \gamma_{0} + \gamma_{1}U_{1j} + \dots + \eta_{j}, \qquad \eta_{j} \sim N(0, \sigma_{\mu}^{2})$$
Eq. 5

where Y represents the condition index of the *i*th individual at the *j*th site (logittransformed in the case of lipid),  $\alpha$  is the individual-level intercept,  $\beta_1 - \beta_3$  are the coefficients for the individual-level variables mass, age, and the interaction between mass and age, respectively. The site-level intercept  $\mu_j$  is informed by the group coefficients  $\gamma_n$ and  $U_{jn}$  is the site-level explanatory variable *n* (i.e., ATUs, density, LW, pool-riffle ratio, elevation, total phosphorus, and gradient). Individual level variation is given by  $\varepsilon_i$  and site-level variation by the residual error  $\eta_j$  which are normally distributed with a mean of 0 and variance of  $\sigma^2$ .

Normality of explanatory variables and heteroscedasticity of residuals were visually assessed using model diagnostic plots (residuals vs fitted values and normal Q-Q) (Lüdecke et al., 2024; Zuur et al., 2010). All statistical analysis was performed using R 2023.12.1 (R Core Team, 2024).

All continuous explanatory variables were standardized and centered by subtracting the mean and dividing by 1 standard deviation. I assessed for multicollinearity among explanatory variables through a Pearson's correlation coefficient matrix, only including variables with absolute correlation coefficient <0.80 (Zuur et al., 2010) (Figure A.2). I also examined different density metrics (*e.g.* effective density, Post et al., 1999) and found the results were not sensitive, and therefore used density (fish/m<sup>2</sup>).

#### Model Selection and Averaging

For each of the three condition metrics, I compared multiple hypotheses using all combinations of variables to determine which habitat variables had the largest effect on each condition metric (Heinze et al., 2018). I used the *dredge* function on a global model of each condition metric to examine all possible combinations of site-level covariates

after removing those with high collinearity. All models included age, mass and an agemass interaction to account for the allometric relationship between mass and condition and the strong positive interaction between age and size.

I used the Akaike Information Criteria for small sample sizes (AICc) to select the top models of the candidate set (Burnham & Anderson, 2002). Smaller AICc values are representative of the highest parsimony without information loss (preventing model overfitting). The top model set was selected using the criteria of  $\Delta$ AICc <2, as  $\Delta$ AICc values greater than 2 mean a significant decrease in model parsimony (Sutherland et al., 2023). AICc was calculated as:

$$AICc = -2\log(L(\theta)) + 2K + \frac{2K(K+1)}{n-K-1}$$

Eq. 6

Where *n* is the sample size,  $-2 \log(L(\theta))$  is the log likelihood estimates of model parameters and K is the number of parameters fit by the model.

I performed model averaging using the top candidate models when there was no clear top model (weights <0.9) (Symonds & Moussalli, 2011, R package *MuMin*, Bartoń, 2024). I calculated model-averaged parameter estimates using the natural-average method, and their 95% confidence intervals (CI) were calculated based on unconditional standard deviation (Burnham & Anderson, 2002). Explanatory variables were deemed to be important if the 95% CI excluded zero. I compared the model averaged conditional coefficients for the relative influence of each variable on the condition metric. I assessed relative variable importance (RVI) by summing the AICc model weights ( $\omega_i$ ) for the variable across all models in the set where it was present (Burnham & Anderson, 2002). Model averaged coefficients were used to calculate predicted condition values.

#### **Evaluation of Condition Metrics**

Condition metrics were assessed for their identification of habitat- condition linkages by determining if the relationship between a condition metric and the important explanatory habitat variables was biologically important within the range of habitat variation measured in this study. Biologically important was defined by a change in energetic condition likely to influence survival outcomes, causing average individuals to approach or fall below predetermined survival thresholds of energetic condition taken from other studies (Birnie-Gauvin et al., 2021; Biro et al., 2004; Hurst, 2007; Mogensen & Post, 2012). Certainty of this relationship was based on prediction accuracy and model fit. I selected a single top model from the  $\Delta$ AICc of <2 candidate set with the fewest parameters based on parsimony to examine prediction accuracy and model fit (Bolker, 2008; Burnham & Anderson, 2002). To determine which condition metric was best described by the habitat variables in the model, I evaluated the hierarchical model predictive performance using root mean squared percentage error (RMSPE), which measures the normalized prediction error (Eq. 7). Lower RMSPE scores indicate better predictive performance.

$$\text{RMSPE} = \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left(\frac{y_i - \hat{y}_i}{y_i}\right)^2 100\%}$$

Eq. 7

Where  $y_i$  denotes the actual observed values, and  $\hat{y}_i$  the predicted values of condition based on the model, and *n* is the sample size.

I also evaluated the variation in condition within and among sites. I calculated the coefficient of variation for each site (standard deviation/ site mean), and the among-site variation (using the across-site standard deviation/ across-site mean).

#### 2.4.2. Seasonal Variation in Energetic Condition

#### Model Description

I assessed seasonal changes in juvenile coho salmon condition for age 0+ and 1+ fish. I calculated the four condition metrics (using percent protein in addition to percent lipid,  $K_n$ , and ED) for individuals across months and separately for each site, examining the change in energy allocation between somatic growth and lipoprotein storage by comparing changes in the proportion of lipid and protein composition (Hurst & Conover,

2003). To test the seasonal hypotheses in Table 1.1, I constructed a linear regression model for each condition metric at each site. I included the main effects of mass and month and their interaction as explanatory variables, centering the data. For percent lipid and protein, a beta distribution with a logit link was used to address the proportion data and a Gaussian distribution was used for the  $K_n$  and ED models. The general model structure is as follows:

$$Y_{ik} = \alpha + \beta_1 Month_k + \beta_2 Mass_i + \beta_3 (Mass_i \times Month_k) + \varepsilon_{ij}$$
$$\varepsilon_i \sim N(0, \sigma^2)$$

Eq. 8

where *Y* represents the condition index of the *i*th individual in the *k*th month (logit-transformed in the case of lipid),  $\alpha$  is the intercept,  $\beta_1$  is the coefficient for month,  $\beta_2$  is the coefficient for mass and  $\beta_3$  is the coefficient for the interaction between mass and month. Month is a categorical variable where *k* is either July, August, September or April. The residual error  $\varepsilon_i$  has a mean of zero and is normally distributed for the *K<sub>n</sub>* and ED models.

I calculated the month-specific relationship between condition and mass separately for each site. I calculated the monthly mean condition for an average-sized fish using the intercept  $\alpha$  and the month-specific coefficients ( $\beta_1$ ) for each site. I then extracted the month-specific slope (calculated from  $\beta_2$  and  $\beta_3$ ) to examine how slope differs across the months for each site. This allowed me to determine the change in mean condition per mean mass over time (intercept), as well as the change in the allometric relationship between condition and mass over time (slope). Significance of the differences across months was tested using a pairwise t-test with a Bonferroni correction to account for family-wise error rate occurring with comparing multiple months at once (Lee & Lee, 2018).

### 3. Results

#### **3.1.** Among-Site Variation in Energetic Condition

Juvenile coho salmon energetic condition and rearing environments varied among the 13 study streams (Table A.3, Table A.4). Across all sites, whole-body percent lipid (lipid) ranged from 1.03-9.85 (%), relative condition factor ( $K_n$ ) from 0.78-1.17, and energy density (ED) from 3.33-7.91 (kJ g<sup>-1</sup>). There was greater variation among sites than within sites for all condition metrics (percent lipid: within site CV = 5.6-10.9%, among site CV = 20.3%;  $K_n$ : within-site CV=0.88-2.38%, among-site CV= 3.2%; ED: within site CV = 1.7-3.4%, among site CV = 6.5%).

#### 3.1.1. Individual fish size and condition metrics

Larger fish had higher energetic condition levels. Percent lipid, relative condition factor ( $K_n$ ), and energy density (ED) increased with fish mass, and mass was an important predictor in all models for the three condition metrics. Fish mass across all sites ranged between 0.8-16.3 g (Table A.4). There were clear and consistent effects of age and mass and their interaction on all condition metrics. Allometric scaling of energetic condition (energy density and percent lipid) to mass appeared nonlinear, and was characterized by an interaction between mass and age. The effect of mass for all condition metrics was more uncertain for Age 1+ fish than Age 0+ fish, likely due to a difference in sample size (n=270 for Age 0+ samples, n=81 for Age 1+ samples). In all condition models, the effect of mass was multiple times greater than the effect of top habitat variables (4x for lipid, 6x for  $K_n$ , 6x for ED, Figure 3.2).



Figure 3.1. The age-specific relationships between each condition metric and the significant variables from the hierarchical model. The regression line and 95% confidence area of the model-averaged coefficients are shown for each condition metric: Top Row: Percent lipid and A) Mass, B) Large Wood (LW), C) Accumulated Thermal Units (ATUs), Middle Row: Le Cren's relative condition factor (*K<sub>n</sub>*) and D) Mass, E) LW, F) Gradient, and Bottom Row: Energy Density (ED) and H) Mass, and I) Total Phosphorus. Triangles, solid regression line and darker 95% confidence region shading represent the Age 1+ fish, while circles, dashed regression line and lighter 95% confidence region shading represent Age 0+ fish.
#### **3.1.2.** Linking fish energetic condition to habitat variables

#### Juvenile Percent Lipid

Juvenile coho salmon sampled from cooler streams had higher percent lipid than fish from warmer streams (Figure 3.1). For example, for every additional 3°C difference in mean temperature between two streams over 30 days (90 ATUs), I estimated percent lipid would decrease by 1.17% in an average sized fish. This is within the observed variation of ATUs observed among sites (the difference between the warmest and coolest sites). Accumulated thermal units had the largest effect on percent lipid of all the habitat variables considered (Figure 3.2.A) and was present in all models in the candidate set (RVI=1.0). Although large wood (LW) appeared to have a similarly large effect on percent lipid as ATUs, the direction of the effect was sensitive to inclusion of one site (Fennell) and its removal resulted in a weakly positive effect (95% confidence limits crossed 0). Accumulated thermal units (ATUs) was the only habitat variable included in the top model ( $\Delta AICc = 1.84$ ) (Table 3.1). The remaining habitat variables were not present, or common within the top candidate set of models for percent lipid (in one or fewer models) and parameter estimates were highly uncertain (Table A.5). Notably, there was a lack of effect of juvenile coho salmon density on percent lipid (95% confidence interval crosses zero, Figure 3.2.A).

## **Relative condition factor** (*K<sub>n</sub>*)

Juvenile coho salmon had higher relative condition factor ( $K_n$ ) in higher gradient streams compared to lower gradient streams (Figure 3.1). Gradient had the largest effect on  $K_n$  among all the habitat variables considered (Figure 3.2.B). Model-averaged predictions indicated that a 4.09% increase in gradient (from low to high) while holding all other variables constant resulted in a 0.03 increase in  $K_n$  for an average fish. This indicates that the maximum change in gradient seen in this study system would result in a marginal 3% increase in fish condition. Like lipid, LW appeared to have a similarly large effect on  $K_n$  as gradient, however the effect size and direction were sensitive to the inclusion of the same site (Fennell). Gradient had the highest RVI score of 1.0 and was present in all three of the  $\Delta$ AICc<2 candidate models (Table 3.1). The mean  $K_n$  at most

sites is less than one, suggesting that the fish sampled in September 2020 had lower relative mass compared to the average individuals of the same length measured during September in other years from the same population (all 13 sites combined). Remaining habitat variables were not present or common in the top candidate set for  $K_n$  (one or less models), and parameter estimates were highly uncertain (Table A.5). Notably, ATUs and density have very little to no effect on  $K_n$ .

## **Energy Density**

Juvenile coho salmon had higher energy density (ED) in streams with higher total phosphorus (TP) concentrations (Figure 3.1). This proxy for nutrients had the largest effect on ED of all habitat variables considered. Based on model-averaged predictions, increasing TP by 12.13  $\mu$ g/L (from lowest to highest recorded site levels) would result in an ED increase of 0.38 kJ/g for the average fish. In other words, the ED of an average fish would increase by 6.9% with a shift in TP from lowest to highest value measured across sites. Total phosphorus had an RVI of 0.88 and was in 10 of the 12 models averaged in the  $\Delta$ AICc <2 top model set (Figure 3.2.C). Total phosphorus (TP) was the only explanatory habitat variables were not present, or common within the top candidate set for energy density (in five or less models) and parameter estimates were highly uncertain (Table A.5). Like *K<sub>n</sub>* and lipid, I observed no effect of density on ED.



Figure 3.2. Standardized model-averaged coefficients (points) with 95% conditional confidence intervals (lines) for condition metrics A) percent lipid, B) Le Cren's relative condition factor (*K<sub>n</sub>*), and C) energy density (ED). Explanatory variables are presented for each response variable in decreasing order of their Relative Variable Importance (RVI) value (indicated on right). An asterisk (\*) beside the RVI value indicates the variable was fixed to be included in all models (age, mass and the age-mass interaction).

## **3.1.3.** Comparison of condition metrics

Models describing the different condition metrics differed in their prediction error. The condition metric that was best explained by habitat variables in the top model was relative condition factor ( $K_n$ ), as indicated by the lowest prediction error (Table 3.1). The top percent lipid model had the highest prediction error by a large margin, while  $K_n$ and ED showed relatively high prediction precision. I assessed model performance of each of the condition metrics using root mean squared percentage error (RMSPE). The top lipid model had an RMSPE of 33.78%, compared to the 5.32% RMSPE for  $K_n$  and 7.21% RMSPE for ED. The top lipid model (including habitat variables) still performed better (33.78% RMSPE) than models with only site effect (56% RMSPE), and with site effect and mass (37% RMSPE). This indicates that habitat variables do play a descriptive role in lipid, despite the high model error. Including an interaction term with age improved the predictive performance of the models across all condition indices, especially for lipid. When only Age 0+ fish were modelled, the error decreased notably to 27% RMSPE. This lower error suggests that the model's accuracy improves for this age group.

I also assessed the correlations among condition metrics, finding that condition metrics were moderate to strongly correlated with each other (Figure A.4). As expected, there was a strong positive relationship between percent lipid and ED (Pearson's correlation coefficient=0.90). The relationships between  $K_n$  and both percent lipid and energy density were moderately positive (Pearson's correlation coefficient for lipid=0.48, ED =0.44). Table 3.1.Top models (selected as the least complex model within ΔAICc < 2)<br/>from modelling juvenile condition using three metrics. Aikaike<br/>information criterion (AIC) corrected for small sample size (AICc)<br/>was used to determine top model. Note mass, age and mass:age<br/>interaction were included in all models during selection process. All<br/>models contain a site-level intercept informed by site-level habitat<br/>variables.

Condition Metric	Model Parameters (fixed effects only)	dfª	logLik <sup>b</sup>	AICc <sup>c</sup>	<b>AAICc</b> <sup>d</sup>	ω <sub>i</sub> e	RMSPE
Percent lipid	Lipid ~ Age + ATU + Mass + Age:Mass	7	1,136.03	-2,257.73	1.84	0.14	33.78
Kn	$K_n \sim Age + Gradient +$ LW + Mass + Age:Mass	8	552.29	-1,088.16	0.00	0.55	5.32
Energy Density	ED ~ Age + Mass + TP + Age:Mass	7	-146.65	307.75	0.00	0.15	7.21

**a**. Degrees of freedom, **b**. Log Likelihood, **c** AICc score of the top model, **d**.  $\Delta$ AICc is the difference in AIC values between model and the lowest AICc ranked model in the suite, **e**.  $\omega$ i is the Akaike weight, the probability that a model is the most parsimonious model of the set **f**. RMSPE is the root mean squared percentage error, as a percentage at the scale of the condition metric. All models included age, mass and an age-mass interaction.

## **3.2.** Seasonal Variation in Energetic Condition

Overall, fish energetic condition decreased throughout the summer, and again over winter (Figure 3.3). Though most changes in average percent lipid and protein, relative condition factor ( $K_n$ ) and energy density (ED) across months are largely insignificant with pairwise comparisons, there is a consistent trend of decreasing condition from July 2022 to April 2023 (Table A.6). Because values were centered, the intercept and month coefficients represent the monthly average for the modelled condition. The allometric relationships between size and condition metrics (represented by the month and condition-specific slope coefficients) appears to be positive for all condition metrics but are highly uncertain. Given the results from the among-site variation analysis showing the strength of the allometric relationship between size and lipid percent, the uncertainty in the temporal analysis may be an artifact of the small sample size used in this analysis (Figure A.5).



Figure 3.3. Percent lipid, percent protein, Le Cren's relative condition factor (K<sub>n</sub>) and Energy Density (ED) coefficients across months for the Cedar, Reg Christie and Tum Tum sites, with 95% confidence intervals. The coefficients were calculated for each site using a base linear regression model of condition with predictors mass, month and a month-mass interaction (Eq. 8). The intercept plots (A, C, E, G) represents the condition level for an average-sized fish for each month while the slope coefficient plots (B, D, F, H) represent the condition specific change with an increase in fish mass. The black dashed line in the slope plots represents the zero line, which indicates no relationship between condition and mass.

## Percent lipid

Whole body percent lipid was the highest in July and tended to decrease during summer and again over winter (Figure 3.3A). Lipid declined between July and September at all sites (Cedar = -1.24%; Reg Christie = -1.42%, Tum Tum = -1.31%) (Table 3.2). The over winter decline in mean percent lipid (September-April) was similar to the summer decrease (Cedar = -1.27%, Reg Christie = -0.67%) (Table 3.2). Cedar had slightly higher lipid values in September compared to Reg Christie and both sites had high within-site variance compared to other months (CV: Cedar = 10.1%, Reg Christie=9.1%). In April, mean percent lipid varied minimally both within-site and between the two sites (CV: Cedar = 4.6%, Reg Christie= 0.4%). Pairwise differences between July and September were significantly negative at all sites, and at both Cedar and Reg Christie pairwise differences between September and April showed another significant decrease in average lipid (Table A.6). Larger fish allocated more energy to lipids compared to smaller fish. This pattern of size-dependent energy allocation was consistent during the summer months but significantly reduced in April (Figure 3.3B, Table A.6, Figure A.5). The change in the lipid-mass allometric relationship is only significantly different in between April and the summer months, but not within the summer months at Cedar and Reg Christie (p-value< 0.001).

Table 3.2.Condition metric measurements with standard deviation (percent<br/>lipid and protein, relative condition factor  $(K_n)$ , and energy density)<br/>across three sites between the months of July to September 2022, and<br/>April 2023, with standard deviation. The samples used for lipid<br/>analysis and  $K_n$  are noted by n, while the samples that were also used<br/>for energy density analysis are noted in brackets.

Site	Month	n	Mean Lipid (% gg <sup>-1</sup> weight)	Mean Protein (% gg <sup>-1</sup> weight)	Mean K <sub>n</sub>	Mean Energy Density (kJg <sup>-1</sup> )
Cedar	July	15 (15)	$5.01\pm0.16$	$15.82\pm0.17$	$0.98\pm0.02$	$5.72\pm0.07$
Cedar	August	15 (14)	$4.64\pm0.23$	$16.09\pm0.12$	$0.99\pm0.02$	$5.68\pm0.09$
Cedar	September	15 (10)	$3.77 \pm 0.38$	$15.88\pm0.11$	$0.94\pm0.02$	$5.40\pm0.15$
Cedar	April	15 (11)	$2.52\pm0.09$	$15.41\pm0.12$	$0.85\pm0.02$	$4.62\pm0.06$
Reg Christie	July	15 (12)	$4.50 \pm 0.21$	$15.36\pm0.10$	$1.01\pm0.02$	$5.45\pm0.09$
Reg Christie	August	15 (10)	$3.38 \pm 0.23$	$16.09\pm0.16$	$0.93\pm0.04$	$5.09\pm0.12$
Reg Christie	September	15 (13)	$3.08 \pm 0.28$	$15.68\pm0.17$	$0.94\pm0.01$	$4.96\pm0.13$
Reg Christie	April	15 (9)	$2.41\pm0.10$	$14.88\pm0.24$	$0.81\pm0.04$	$4.47\pm0.10$
Tum Tum	July	16 (14)	$4.42\pm0.21$	$15.65\pm0.12$	$1.04\pm0.02$	$5.49\pm0.09$
Tum Tum	August	15 (14)	$3.54 \pm 0.28$	$16.20\pm0.14$	$0.94\pm0.03$	$5.28\pm0.11$
Tum Tum	September	15 (14)	$3.11\pm0.25$	$15.50\pm0.18$	$0.94\pm0.03$	$4.93\pm0.13$

## Percent protein

Whole body percent protein remains relatively constant over months and across sites. The average percent protein changed marginally throughout the summer months, increasing slightly at Cedar and Reg Christie (Figure 3.3C). (Cedar = 0.06%, Reg Christie = 0.32%, Tum Tum = -0.15%) (Table 3.2). The decline in percent protein over winter was more notable than changes during the summer, though variation was overall much less than percent lipid (Cedar = -0.41%, Reg Christie = -0.48%) (Table 3.2). There was a marginally significant difference in percent protein between September and April for Cedar and Reg Christie (Table A.6). Larger fish do not appear to allocate more energy to protein than smaller fish (Figure 3.3D). The direction of the allometric relationship between protein and mass was inconsistent across months (fluctuating between a positive and negative relationship) and uncertain (95% CI crossed zero) (Table A.6, Figure A.5).

## Relative condition factor (K<sub>n</sub>)

Relative condition factor ( $K_n$ ) tended to decrease from July to April. A decrease in  $K_n$  between July and September was consistent across all sites (Cedar = -0.04; Reg Christie = -0.07, Tum Tum = -0.10) (Figure 3.3E).  $K_n$  decreased further from September to April at Reg Christie and Cedar (Cedar = -0.09; Reg Christie = -0.13) (Table 3.2). Across all sites, there were consistently significant pairwise differences in mean  $K_n$  between summer months and April, but insignificant variance in  $K_n$  between the summer months (Table A.6). As expected, larger fish had higher  $K_n$  than smaller fish in all months, shown by a consistent weak positive allometric relationship between  $K_n$  and mass (Figure 3.3F, Figure A.5).

## Energy Density

Juvenile coho salmon energy density (ED) consistently declined from July to April. Energy density for an average fish at all sites decreased throughout the summer between July and September (Cedar = -0.32 kJ/g, Reg Christie = - 0. 49 kJ/g, Tum Tum = -0.56 kJ/g) (Figure 3.3G, Table 3.2). Overwinter ED decline was higher for Cedar, and the same as the summer decline for Reg Christie (September-April: Cedar = -0.78 kJ/g, Reg Christie = -0.49 kJ/g (Table 3.2). The changes in average ED across different sites and months reveals several significant seasonal effects between July and April, and September and April (Table A.6). I observed a consistent pattern of seasonal variation in energy density across all sites, with particularly pronounced differences between summer months and April. Overall, ED increased with fish size, though this relationship was weakest in April with fish of all sizes displaying similar ED values and the slope coefficient close to 0 (Figure A.5). The positive allometric relationship between ED and body size varies minimally, only decreasing in April at Cedar and Reg Christie (Figure 3.3H). All month-specific allometric relationships with energy density are positive but uncertain, and the trends across months suggest that there are not significant seasonal effects on the allometric relationship between energy density and mass.

# 4. Discussion

# 4.1. Overview of key findings

An individual's energetic condition is shaped by the interplay between physiological processes and habitat-driven energetic availability and costs. Physiological metrics can be used as an integrated measure connecting individual energetic condition to habitat usage (Beerens et al., 2015; Gaillard et al., 2010). This study investigated changes in juvenile coho salmon energetic condition in response to among-site and temporal variation in freshwater rearing habitat. While other studies have measured variation in overall salmonid condition in different habitats or seasons (Biro et al., 2004; Næsje et al., 2006), few have explicitly connected variation in individual energetic condition to measured habitat variables and seasonal changes in a field study system. Using three physiological measurements (percent lipid, percent protein and energy density) and one morphometric measurement (relative condition,  $K_n$ ), fish size was the best descriptor of the variation in all condition metrics but accounting for month and site-level variation in habitat improved understanding of fish energetic condition. In my among-site analysis, variation in juvenile coho salmon condition among sites was related to differences in habitat, supporting my first hypothesis. Different habitat variables explained each of the three condition metrics (temperature-percent lipid, gradient- $K_n$ , and nutrients-ED). This suggests that these metrics may represent different aspects of individual fish condition or reflect different sensitivity to habitat variation (e.g. temperature, productivity, habitat complexity, nutrients).

As hypothesized, my temporal analysis found variation across months in juvenile coho salmon energetic condition with a pronounced decrease in all condition metrics after winter. However, contrary to my predictions and previous literature (Biro et al., 2021; Cleary et al., 2012; Mogensen & Post, 2012), all metrics of energetic condition decreased over summer. Decreased energetic condition throughout the summer months provides novel insight into the seasonal variation on juvenile coho energetic condition and importance of accounting for site-specific temporal variation. Taken together, the among-

site and temporal study results suggest that juvenile coho energetic condition is driven by the interplay between individual physiological traits and habitat factors.

# 4.2. Linking fish energetic condition with among-site habitat variation

Cooler stream temperatures were associated with higher percent lipid in juvenile coho salmon, suggesting that temperature strongly influences fish energetic condition among sites. Water temperature plays a significant role in the physiological regulation of fish, particularly concerning metabolism (Araújo et al., 2023; Brett, 1952, 1971; Fry, 1971; Volkoff & Rønnestad, 2020). The energetic requirements for metabolic processes, growth, and energy storage are temperature-dependent, meaning that physiologically taxing temperatures can reduce the surplus energy available for storage or growth. My findings align with previous studies that have demonstrated an inverse relationship between temperature and energy storage in juvenile salmonids, where colder environments tend to result in higher lipid content and larger fish size over time (Ahti et al., 2020; Feldhaus et al., 2010; Kammerer & Heppell, 2013). Kammerer and Heppell (2013) further concluded that temperature was the most significant factor influencing habitat quality for salmonids over their two year study, even more so than nutrient availability. Lower temperatures could be a useful indicator of higher habitat quality or reflect energetic allocation strategies that promote lipid storage. Berg et al. (2011) found a marked increase in salmonid lipid storage in rivers along increasing elevation and latitude gradients, reflecting variation in overwintering lipid storage strategies likely governed by energetic demands from temperature or winter length. My results indicate that a 3-degree increase in the average daily temperature (increasing from 11°C to 14°C) over a 30-day period would reduce whole-body percent lipid from 3% to 1.8% (a 1.2% decrease) in an average fish. Notably, both of these temperatures (11°C and 14°C) are well within the optimal temperature range for juvenile coho salmon (Brett, 1952; Coutant, 1977). A 1.2% reduction in lipid could indicate decreased survival likelihood for over 29% of the fish sampled in my study with measured percent lipid at or below 3%, given the critical 1.5-2% lipid survival threshold reported in both field and laboratory studies (Biro et al., 2004; Wilson et al., 2021). Increased mortality rates for this

proportion of the population due to lipid loss could lead to measurable declines in population size.

Salmon are sensitive to minor temperature changes, with this sensitivity potentially being intensified by nutrient or resource limitations (Breau, 2013). Juvenile coho salmon are known as the most temperature-intolerant of the Pacific salmonids, with optimal rearing temperatures likely ranging between 11 and 16°C, although this can depend on food availability (ration) (Brett, 1952; Richter & Kolmes, 2005). My findings support the literature suggesting that temperature changes can strongly affect individual fish physiology, with the potential to impact survival and consequently have populationlevel effects (Jonsson et al., 2012; Kaylor et al., 2019; Railsback, 2022). The strong link between percent lipid and temperature in my study highlights the importance of considering water temperature when evaluating habitat quality. This is particularly pertinent given the measured increases in river temperatures in anthropogenicallyimpacted interior BC systems (Bradford & Irvine, 2000; Cunningham et al., 2023; Macdonald et al., 2003). In nutrient-poor environments, temperature may have a stronger impact by increasing metabolic demand beyond energy intake (Araújo et al., 2023; Brett, 1971). Elevated summer temperatures can further strain fish in these systems, leading to a decline in energetic condition (Volkoff & Rønnestad, 2020). Examining interactions between temperature and nutrient levels on fish energetic condition should be a focus of future research.

Total phosphorus emerged as the best habitat predictor of energy density (ED) in juvenile coho salmon, indicating a relationship between site productivity and individual fish energy stores. This relationship is particularly relevant given that many streams in my study system are considered nutrient-poor (Naman, unpublished, Kaylor et al., 2019). My finding that ED is best represented by total phosphorus aligns with other research demonstrating similar links between nutrient availability and energy dynamics in aquatic ecosystems (Bartels et al., 2012; Biro et al., 2021; Marcarelli et al., 2011). Lapointe et al. (2016) found that total phosphorus was a strong predictor of fish biomass in rivers and lakes across Canada, indicating importance of nutrients for fish productivity in aquatic systems. While the variation in ED seen across my study system was not large, my

findings indicate that nutrient concentrations likely play a role in explaining variation in fish energetic condition across habitats. However, further work is needed to develop linkages between nutrients and fish condition (Ouellet et al., 2024). As a broad measure of habitat energy availability, total phosphorus may not entirely capture the scale of effect that habitat productivity has on juvenile coho salmon energetics. More direct measurements of habitat productivity such as primary or secondary production, ration, or studying food web energy transfer could better capture the relationship between fish condition and habitat energy availability (Naman et al., 2022; Saunders et al., 2018). Ultimately, my findings support that increased nutrients (indicative of habitat productivity) are linked to increased energetic condition in fish and may be a key component in determining optimal habitat for juvenile coho salmon.

Although higher percent lipid and  $K_n$  values were associated with lower concentrations of large wood (LW) in the system, this result is likely misleading and of minimal biological significance. The negative association is heavily influenced by a single site and its exclusion from the analysis leads to a weakly positive effect, suggesting high uncertainty in the relationship. My findings are consistent with other studies that have similarly found no significant correlations between LW and overall fish condition, survival (Ebersole et al., 2006), increase in overall body size, or population abundance (Walls, 2020). This supports that large wood may be connected to key habitat variables for salmon (*e.g.* energetic and predator refuge and prey availability), but it does not solely explain variation in individual fish condition.

September juvenile coho salmon density did not explain individual energetic condition, indicating a decoupling between individual condition and conspecific numbers at the temporal or among-site scale of my study. Measuring population density may not always reflect individual energetic condition and long-term population dynamics (Bailey et al., 2018; Chaparro-Pedraza & de Roos, 2019; Myrvold & Kennedy, 2015a; Rosenfeld, 2014). The influence of density-dependent versus independent factors on individual energetic condition appears to vary depending on species biology and habitat. Other studies have shown that the strength of density-dependent processes on the connection between habitat and fish populations varies over space and time, playing a smaller role at

certain life stages or at a smaller scale (Bailey et al., 2018; Grossman & Simon, 2020; Myrvold & Kennedy, 2015a).

Density-dependent processes may have already occurred during my among-site study in September, explaining the small positive correlation between density and condition metrics that contradicted the negative relationship I had predicted. Higher density could loosely reflect the availability of energetic resources, with potentially density-independent biotic and abiotic factors (e.g. temperature and nutrient availability) more strongly impacting individual energetic condition (Hodgson et al., 2017; Myrvold & Kennedy, 2015b). For example, Bradford et al. (1997) found that large-scale habitat features like stream length could predict smolt abundance at a regional level over time, but for an individual stream, local habitat features did not explain variation in abundance. On the other hand, Ebersole et al. (2006) found that overwinter juvenile coho salmon survival within a stream was more closely linked to fall size and body condition than to density-dependent factors like competition. These findings suggest that while density can help understand population dynamics, individual energetic condition may be a more sensitive indicator of habitat changes over shorter timescales, smaller areas or during certain life stages. Further research across different systems and timescales is needed to clarify the role of density-dependent processes in regulating individual energetic condition and its impact on survival and population dynamics.

Individual fish size drives many traits predictive of higher survival, including energetics and growth (Ahti et al., 2020). Other studies observed a strong positive relationship between fish size and proxies of survival (*e.g.* energetic condition) (Brett, 1965; Martin et al., 2017; Post & Parkinson, 2001). My findings support this relationship, where individual mass was multiple-fold more explanatory for all condition metrics compared to habitat variables. Smaller fish are more likely to die under starvation conditions due to metabolic allometry (Biro et al., 2004; Brett, 1964; Post & Parkinson, 2001). Smaller fish have higher rates of growth, food consumption and respiration in addition to higher risk of predation compared to larger fish. Therefore, the competing strategies of allocating energy to growth versus energy storage depends on both individual fish size and habitat-specific mortality pressures (predation versus starvation)

(Reinhardt, 2002). The disproportionate effect of survival pressures on smaller fish is particularly pertinent when considering the impact of temporal variation in energetic habitat demands (e.g. increased temperature, decreased productivity) on individual fish energetic condition. I attempted to address the shift in energetic condition across seasons while accounting for this allometric relationship between condition and size in the next part of the study.

# **4.3.** Linking fish energetic condition with seasonal habitat variation

Contrary to my hypothesis, condition decreased throughout the summer months. This finding was consistent across all three sites and condition metrics. Percent lipid and energy density showed the largest decrease in energetic condition, though relative condition factor ( $K_n$ ) also decreased marginally throughout the summer. Protein levels remained stable throughout the sampled months, supporting previous findings that energetic variation in fish is largely attributed to storage lipids (Jonsson & Jonsson, 1998, 2003; Martin et al., 2017). Seasonal site variation occurring between July and September appears to result in net negative energy in juvenile coho salmon during the summer at these sites, a typically net positive energy and growth period (Biro et al., 2021; Cleary et al., 2012; Mogensen & Post, 2012). This decline in energetic condition occurred even though temperatures did not reach levels normally defined as stressful for juvenile salmonids, suggesting that summer may be a time where food availability at these sites is inadequate for meeting the metabolic demands of individual fish.

The shared pattern of decreased energetic condition in individual fish across sites indicates a shared influence of temporal habitat variation on energetic condition. In many species, juvenile energetic condition increases with body size and fluctuates seasonally, with energy stores increasing the fastest during transitions between favourable and unfavourable periods (Martin et al., 2017). My results showing an overall decline in energetic condition through summer (but higher energetic condition in July compared to April) suggests that spring may be an energetically favourable period while summer is energetically demanding in this study system. This result contrasts formerly observed

patterns of increasing lipid from summer to autumn in freshwater temperate fish (Cleary et al., 2012; Mogensen & Post, 2012; Post & Parkinson, 2001), but is similar to juvenile coho salmon growth patterns in wetland habitats in the North Thompson watershed (Milner, 2023). Given that fish in these systems appear to retain high site fidelity (Braun, unpublished), there are a few possible explanations for this result.

First, the unexpected finding of decreased energetic condition throughout the summer could be attributed to the combined effects of rising temperatures and reduced food availability culminating in both increased fish metabolism and a decline of habitat quality (Brett & Groves, 1979; Rashidabadi et al., 2022). Temperatures at the study sites are typically within the optimal range for juvenile coho salmon (remaining under 16°C) making reduced energetic condition due to thermal stress unlikely (Brett, 1952). However, cumulative summer temperatures at these sites may increase metabolic demand to the point where available energy in these resource-limited sites is insufficient, resulting in overall decline in energy stores and subsequently energetic condition (Brett, 1952; Railsback, 2022; Willey, 2004). Temperature can affect salmonid feeding behaviour, where minimal increases in temperature cause salmon to occupy colder microhabitat with decreased prey resources (Gallagher et al., 2022; Kaylor et al., 2019; Saunders et al., 2018). For juvenile coho, temperatures higher than 15 °C can change habitat selection behaviour (Konecki et al., 1995) and negatively affect growth rates (Willey, 2004), particularly in food-limited systems. In a global meta-analysis of climate effects on salmonid productivity, Gallagher et al. (2022) determined that higher temperatures reduced salmonid feeding activity during the warmest time-periods, leading instead to thermal refuge-seeking behaviour. Salmon expending more energy on metabolic costs while reducing energy intake from their habitat ultimately leads to less surplus energy allocated to either growth or storage. The decline in energetic condition seen in my study could be attributed to this combination, though further research is required. This emphasizes the importance of considering both biotic and structural habitat aspects, as well as possible interactions between habitat variables in determining habitat quality.

Second, seasonal food availability in these systems may also contribute to the unexpected seasonal pattern of energetic condition decline. Many studies linking fish

energetic condition and productivity have focused on lake systems, while riverine systems may have different patterns of peak productivity, particularly in oligotrophic, higher latitude streams (Biro et al., 2021; Mogensen & Post, 2012; Myrstener et al., 2021). Juvenile coho salmon in small streams feed primarily on benthic invertebrates suspended in flow, though terrestrial invertebrates provide key energetic input for salmonids (Chapman, 1966; Fausch, 1984; Naman et al., 2018). Temporal variation in nutrient availability to aquatic primary producers is emerging as a driver of seasonal energetic availability at higher trophic levels (Benjamin et al., 2022; Lapointe & Rasmussen, 2016; Naman et al., 2022). Myrstener et al. (2021) found aquatic productivity in Arctic streams was seasonally offset from terrestrial nutrient concentrations, where nearly half (48%) of annual productivity in nutrient-poor Arctic streams occurred during the shoulder seasons (spring and fall), with sharp nutrient declines during the terrestrial growing season (summer). Timing of aquatic productivity and energy available in the system is related to fluctuations in temperature, light, and nutrient availability. Further research on the seasonal response in growth and energetic condition in response to measured changes in habitat (e.g. temperature and food availability) during critical timeperiods will contribute to knowledge on how temporal variation influences habitat quality in this system (Armstrong et al., 2021).

As expected, a large decrease in energetic condition occurred over winter between September and April. Winters in this study system can be dry and cold, with air temperatures below zero and precipitation accumulating as snow (Déry et al., 2012). The variation in energetic condition levels across favourable growth periods and energetically taxing stages like overwintering is a ubiquitous phenomenon previously studied in many juvenile fish species (Berg & Bremset, 1998; Biro et al., 2021; Martin et al., 2017; Mogensen & Post, 2012). Overwinter mortality is attributed to significant, often lethal declines in energy storage in fish populations (Biro et al., 2004, 2021). Smaller and younger fish tend to have lower lipid reserves and higher overwinter mortality compared to larger, older fish (Post & Parkinson, 2001). Most fish in my study sampled in April had low lipid percent that fell below 2% but were higher than 1%, reinforcing the hypothesis of a minimum energetic threshold for survival in salmonids observed in other studies (Biro et al., 2004; Næsje et al., 2006; Wilson et al., 2021). The hypothesized survival threshold of 3.5-4 kJ/g energy density is also supported by my findings, with most fish in April near this threshold, and none below (Crossin et al., 2004; Wilson et al., 2021).

Further study establishing a minimum energetic threshold required to survive overwinter could lead to improved understanding of survival and energetic requirements. Physiological determination of survival thresholds may be a useful tool in conservation studies in addition to population measurements. For instance, instead of assuming constant fish condition within a population over time (Breck, 2008), fall surveys of juvenile coho density could be supplemented with physiological assessments of energetic condition to more accurately understand population status. Depending on the season sampled, population density estimates could produce misleading results by failing to capture survival probability of individuals given their energetic condition (Biro et al., 2021). Tagging fish at various energetic condition levels and tracking their overwinter survival could help link individual condition to population-level outcomes. This would clarify how energetic condition affects survival during energetically-taxing periods and improve understanding of the impact of habitat variation on populations. Overall, my results highlight the importance of considering temporal variance in energetic condition when assessing population dynamics in conservation studies to account for changes in energetic demand and availability in habitat over time.

## 4.4. Integration of condition metrics

My findings support that each condition metric—lipid content, relative condition factor ( $K_n$ ), and energy density (ED)—reflects different aspects of energetic condition and accumulation in juvenile fish in relation to habitat variation. Simply put, percent lipid (above the minimum required for structural cell integrity) represents energetic allocation to storage, while energy density represents the net energy intake. Relative condition ( $K_n$ ) is a population-specific morphometric measurement of energetic condition reflected through differences in relative mass for a given fish length. Therefore, each metric may communicate different information about individual energetic condition. The utility of implementing each of these metrics in future studies depends on how each metric reflects energetic condition (and potentially predicts survival), in addition to balancing factors

like cost, time, and predictive performance (Brosset et al., 2023; Lloret et al., 2013; Trudel et al., 2005; Weber et al., 2003).

Measuring percent lipid could be useful for examining energetic allocation strategies and energy storage required for survival during periods of food scarcity or high metabolic demand, such as overwintering or migration. Physiological metrics like percent lipid and energy density (ED) require more intensive sampling and analysis in addition to higher processing cost with the laboratory procedures compared to simple morphometric measurements. Additionally, the high predictive error of the lipid model in my study suggests lower predictive performance, reducing confidence in linking habitat variation to changes in lipid condition. However, this could also indicate a higher sensitivity to other unmeasured factors (e.g. environmental or genetic) potentially impacting energetic condition, which would contribute to the unexplained variation and decrease in predictive performance. Plus, calculating percent lipid and protein required conversion factors with unaccounted-for variation, as the initial raw values had standard errors associated with the multiplied mean values. Despite this uncertainty, percent lipid responded measurably to changes in habitat, with a biologically significant shift in condition based on measured variation in temperature. With further study, this metric could be valuable for identifying individuals at risk of lethal energy depletion, offering insight into how environmental changes or shifts in seasons could affect future population dynamics. Improved understanding of energy storage could help predict survival under specific ecological pressures, like habitat degradation or climate change.

Relative condition factor  $(K_n)$  is a non-invasive morphometric measure of overall and energetic condition that is ideal for large-scale studies. It allows researchers to assess the impacts of habitat changes on fish populations over time, as demonstrated by my temporal study. By evaluating the proportion of individuals with above-average condition,  $K_n$  facilitates population assessments without the need for lethal sampling. However, unlike percent lipid and energy density (ED),  $K_n$  reflects differences in fish shape rather than direct changes in energy reserves, rendering it less sensitive to variations in physiological condition. In my study, measuring  $K_n$  was the most straightforward and cost-effective method, and the among-site model had the lowest

predictive error among the three metrics. However, the low variation in  $K_n$  across sites and months likely indicates a decreased sensitivity to temporal and among-site habitat variation compared to percent lipid and ED rather than a superior model fit. This is supported by both the minimal changes across sites in the among-site study, and decreased sensitivity to seasonal shifts in energetic condition (as evidenced by a significant decline in lipid mirrored by ED across months while  $K_n$  remained stable). In the among-site study,  $K_n$  was moderately correlated to percent lipid and ED values, suggesting that these metrics are connected but not interchangeable. Together, this indicates that  $K_n$  may not capture fine-scale energy changes or the biological significance of habitat variation, potentially due to its decreased sensitivity to shifts in fish energetic status. Other studies support that  $K_n$  may not be the most sensitive indicator of changes in energetic condition, especially over seasonal periods (Rennie & Verdon, 2008) or among different age classes (Jonas et al., 1996). While morphometric metrics like  $K_n$  can indicate overall body condition related to survival aspects such as swim performance (Wilson et al., 2021) and chronic stress through cortisol concentrations (Brosset et al., 2023), further studies are needed to strengthen the link between  $K_n$  and energetic condition in response to habitat change, thereby enhancing its utility in conservation research.

Energy density (ED) provides a broader view of an organism's total energy stores, (including lipid and protein composition), making it especially relevant when evaluating how habitat and environmental changes could impact fish populations over time. It offers insights into a population's capacity for survival and resilience, particularly during times of stress or resource scarcity. Unsurprisingly, percent lipid and ED were highly correlated in individuals in my study, with variation in ED often well explained by variation in storage lipids as demonstrated in other studies (Martin et al., 2017). ED and percent lipid could provide complementary information for explaining how energy reserves are allocated in juvenile fish, although ED provides a more holistic understanding of total energy reserves by accounting for potential energetic allocation to growth and other physiological processes. While there was overall limited variation in ED measured in my among-site study, if considering the variation to be limited to surplus energy storage (allocated for growth and other processes), then the range in ED could represent a

biologically significant change in energetic condition. For instance, the effect of going from highest to lowest nutrients measured in my among-site study could highly impact the amount of energy stored for overwintering, or for fish growth. However, further study is required to link variation in energy density to survival and growth, to determine population-level impacts.

Measuring percent lipid, energy density (ED), and relative condition factor ( $K_n$ ) each provide a unique perspective on how habitat variation translates to fish energetic condition, furthering the development of tools for quantifying important habitat for juvenile salmon. The selection of the appropriate metric depends on study goals whether focusing on survival thresholds, energy budgets, or population-wide condition. Continuing to explore the relationships among these metrics, particularly in different species and ecosystems, will enhance their utility in assessing population status and informing habitat management efforts.

## 4.5. Limitations and future directions

While this study advances our understanding of the relationship between habitat and the energetic condition of juvenile coho salmon, several limitations must be acknowledged. The ability to detect strong habitat-condition relationships may have been reduced by the resolution of habitat variable measurements and the assumption of minimal fish movement and uniform habitat. For example, using prey availability rather than total phosphorus could provide a more direct link between habitat productivity and coho condition (Naman et al., 2016). Additionally, my study may have oversimplified the complex stream habitat, as unmeasured microhabitat variation within sites likely influences fish condition (Walsworth et al., 2015). Important factors like food availability (ration) (Brett et al., 1969; Jonsson et al., 2012) and photoperiod (Spangenberg et al., 2023), which are known to affect energy storage in juvenile salmonids, were not specifically measured.

Improving the resolution of habitat measurements and tracking individual fish over time could strengthen the findings but would require more intensive monitoring and

different methodologies (Walsworth et al., 2015). Given the unexpected seasonal decline in condition, future research should extend sampling into the winter and early summer to provide a clearer picture of juvenile coho energy acquisition and allocation strategies. Tracking energetic changes throughout the year could clarify the interaction between density-dependent processes and habitat variables. Another important step is linking habitat-driven changes in energetic condition to individual survival and population dynamics. My study quantitatively connected habitat variables to energetic condition under the assumption that energetic condition is representative of survival. To confirm these variables as indicators of habitat quality for juvenile salmon, their impact on survival should be established. For instance, if fall energetic condition predicts overwinter survival, it would strengthen the case for these habitat factors as contributors to habitat quality.

Accurate assessments of habitat, condition, and energy allocation strategies also require consideration of species- and population-specific physiology. Therefore, these findings may be specific to the North Thompson coho salmon Conservation Unit. Nonetheless, the approach used in this study could be applied to further research on ecophysiological dynamics in other species and systems to establish broader ecological patterns. Future studies comparing habitat variability with seasonal condition changes in other coho populations or salmon species would provide valuable insights into the generality of these findings.

# 4.6. Management implications

This study has two management implications for understanding species-specific measurement of habitat quality. First, this study provides a refined understanding of how habitat influences individual energetic condition by using physiological metrics. With further development, conservation studies could implement physiological metrics as a quantitative tool for determining habitat quality. Studying energetic condition and allocation in individual fish improves our understanding of the mechanistic relationship between habitat and fish overall condition (and subsequently survival). Recent research emphasizes the important role of ecosystem processes such as seasonality, food-web

dynamics and life-history patterns in explaining variation in salmon overall condition and abundance (Bilby et al., 2023). Measuring individual energetic condition through physiological metrics could provide detailed information on overall condition at a higher resolution scale within systems, due to the increased sensitivity to habitat variation. Additionally, added insight into the direct physiological consequences of changing habitat variables (e.g. temperature and nutrients) may provide more informative predictions on fish response and provide further confidence in defining habitat quality through these variables. For example, assessing the impact of fluctuating food availability or varying water temperatures on the energetic condition of juvenile coho salmon could improve predictions regarding how habitat restoration or degradation would affect their survival rates. Furthermore, identifying critical energetic thresholds and periods of energy accumulation or deprivation in aquatic systems can enhance our ability to predict population-level responses to ecological disruptions over time. Measuring individual energetic condition within a population following habitat changes and identifying a proportion of individuals at or below critical survival thresholds would improve population-level assessments. Comparatively, frequently used correlative studies monitoring population response to landscape-level assessments of habitat structure can fail to capture nuanced effects of habitat change on individual condition (Bilby et al., 2023; Polivka, 2020). Thus, a strength of this study is the approach of assessing habitat by directly linking habitat indices and season with fish energetic condition.

Second, the mechanistic assessment of habitat-condition linkages across the North Thompson watershed for coho salmon juveniles within a specific Conservation Unit provides unique insight into drivers of energetic condition tailored to a specific watershed, population, and life stage. Developing species- and population-specific models that integrate physiological data with biophysical habitat characteristics could enhance our understanding of how animal energetic condition responds to habitat changes. This is particularly relevant for species with complex life histories, like Pacific salmon, which utilize diverse habitats throughout their lifespan (Birnie-Gauvin et al., 2021; Chaparro-Pedraza & de Roos, 2019). For instance, measuring important habitat variables (*e.g.* temperature or food availability) over time in current juvenile coho salmon habitat in the North Thompson and modelling how variation could either promote higher

energetic condition, or cause individuals to potentially fall below energetic survival thresholds could help with prioritizing habitat conservation for these at-risk populations. This will help inform the creation of management plans and assess habitat viability in the face of climate change and anthropogenic pressures (Tudor et al., 2023).

Identifying key habitat variables like nutrients and temperature and their mechanistic relationships with salmon energetic condition and survival will be critical for planning and evaluating habitat mitigation, restoration, and offsetting efforts. For example, understanding how temperature fluctuations affect metabolic rates and energy allocation in salmon can inform management strategies that prioritize maintaining optimal thermal conditions in freshwater habitats. Given the measurable increase in energetic condition with decreased temperatures, protecting and restoring riparian zones for higher shade cover to promote cooler streams could help improve salmon population condition (Cunningham et al., 2023; Justice et al., 2017). Additionally, recognizing the role of nutrient availability in supporting prey populations can aid in habitat restoration efforts that enhance food resources for juvenile salmon. One proposed method could be artificial nutrient addition in streams to increase energetic resources for salmon, though this method requires further study on long-term effects (Bailey et al., 2018). By focusing on protecting or restoring these key variables, conservation planners can develop targeted interventions that address specific habitat needs, ultimately improving salmon survival and population resilience.

By linking environmental changes to physiological attributes, we can improve conservation strategies by targeting the protection or restoration of critical habitat (Tudor et al., 2023). While this study provides valuable insights, it highlights the need for more detailed research to better understand how habitat characteristics influence fish energetics. These findings could contribute to more effective habitat quality assessments for juvenile coho salmon by considering physiological adaptations and temporal shifts in energy allocation during energetically challenging periods, such as overwintering. Measuring energetic condition could address the limitations of traditional populationlevel methods, through providing higher sensitivity of fish response to the effects of dynamically changing habitats.

# 4.7. Conclusion

Identifying the mechanisms driving individual responses to habitat change is essential for understanding the impacts of current stressors on populations and predicting future effects on energetic condition and survival (Aldridge & Boyce, 2008; Bilby et al., 2023; Patterson et al., 2016; Peacock et al., 2023). The variability in juvenile coho condition metrics observed across sites and seasons in this study highlights the influence of among-site and temporal habitat variation on energetic condition. My findings suggest that juvenile salmon energetic condition is closely tied to seasonal habitat changes, underscoring the importance of specific habitat factors for driving survival and population dynamics through critical life stages like overwintering. This study supports the growing body of work developing ecophysiology tools across species and ecosystems, using individual energetic condition as an indicator of habitat quality. Refining tools and continuing to investigate how habitat variation affects individual and population-level outcomes in other systems will be key to advancing conservation physiology and enhancing habitat management efforts.

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## Appendix.

### **Supplemental Tables and Figures**

#### **Hierarchical Bayesian Closed Mark-recapture Overview**

Juvenile coho salmon density data were provided by the North Thompson Salmon Ecosystem Program. This program conducts annual September surveys for juvenile coho salmon and estimates densities using a hierarchical Bayesian closed mark recapture model (*sensu* Milner, 2023; Braun unpublished).

A total of 18 mark-recapture surveys and 20 index surveys were conducted from 2020 to 2023 (Figure A.1). A mark recapture survey included two capture events on consecutive days using minnow traps. During the first capture event a known number of juvenile coho salmon were captured and marked and during the second capture event the number of marked and unmarked juvenile coho salmon were counted. An index survey included a single capture event where all juvenile coho salmon were counted.

Juvenile coho salmon densities in tributary sites are estimated using a hierarchical Bayesian closed mark-recapture model (HBM) developed by Korman et al. (2016) that was based on Wyatt (2002). The model estimates capture probability for each of the two capture events during the mark-recapture surveys, which are used to estimate abundance and density for each site, as well as hyperparameters. The HBM has two levels where it is assumed there is a hyperdistribution for capture probability common to all sites and capture events and a hyperdistribution for fish density common to all sites. The next level assumes there are capture event specific capture probabilities and site-specific densities. Estimates of capture probability for two capture events were derived from the markrecapture data. For index surveys, when only a single capture event was used, the model draws the capture probability from a hyperdistribution to inform the capture probability of the single capture event.

Covariates for capture probability (no. traps/area surveyed) and density (percent pool area) are included in the model to improve overall model fit and estimation of index

69

sites densities. The model assumes that the capture probability does not change among years, which is reasonable as capture methods were the same throughout the study and area and water level ranges were similar, therefore a year effect was not included (Korman et al., 2016). The model also assumes that capture probability was not different between marked and unmarked fish and that fish size did not affect capture probability. Density estimates include juvenile coho salmon aged 0+ and 1+. Model details, equations and parameters can be found below and in Tables A.1 and A.2.

The observation model estimates site and capture event-specific capture probability during mark recapture surveys as well as hyperparameters. The number of marked fish observed at mark–recapture for site *i* on the second capture event was assumed to be a Poisson distribution and depended on the number of marks released on the first capture event and the capture probability for the second capture event (Table A.1; Table A.2, Eq A.1). The catch for capture event one is determined by the abundance for site *i* and site-specific capture probability for capture event one (Table A.2, Eq A.2). The total catch for capture event two and site *i* is assumed to be a Poisson distribution and determined by the number of unmarked fish and the capture probability for capture event two (Table A.2, Eq A.3). The number of unmarked fish in capture event 2 is computed as the abundance for site *i* minus the total marks applied on capture event 1 for site *i* (Table A.2, Eq A.4).

Capture probability varied across sites and capture events and was determined by the mean of the hyperdistribution of logit capture probability and the hyper distribution of logit capture probability from capture event *j*, site *i*. Capture probability followed a logit hyperdistribution (Table A.1; Table A.2, Eq A.5). A covariate for capture probability was also included (no. traps/area surveyed); this effect was common to all sites (Table A.2, Eq A.5). Equation (A.6) in Table A.2 is considered a random variable that comes from a hyperdistribution of capture probability and follows a normal distribution.

In the process model, the density for site *i* is determined by the mean of the hyperdistribution for log density and the random effect of site on log density (Table A.2, Eq A.7, A.8). Both hyperdistributions were assumed to be normally distributed. A

70

covariate for density was also included (percent pool area); this effect was common to all sites (Table A.2, Eq A.7). The site-specific abundance was computed as the product of the density and area surveyed (Table A.2, Eq A.9).



Figure A.1. Estimated juvenile coho salmon density for all sites sampled in the North Thompson system. Closed circles represent density calculated from mark-recapture model, while open circles represent the density calculated from index collections.

Variable	Description
	Data
<b>u</b> <sub>1,<i>i</i></sub>	Total catch on capture event one for site <i>i</i>
$\mathbf{R}_{1,i}$	Marks applied on capture event one for site <i>i</i>
<b>u</b> <sub>2,<i>i</i></sub>	Unmarked fish detected on capture event two for site <i>i</i>
<b>r</b> <sub>2,<i>i</i></sub>	Marks detected on capture event two for site <i>i</i>
$A_i$	Wetted area of habitat at time of survey for site <i>i</i>
$X1_i$	Trap density of specific capture event for site <i>i</i>
$X2_i$	Percent pool habitat for site <i>i</i>
	Month Specific Parameters
$\Theta_{j,i}$	Estimated capture probability for capture event $j$ for site $i$
$\lambda_i$	Transformed hyperparameter for random effect of site on log density
	Hyper Parameters
$\beta_{0i,i}$	Hyperdistribution of logit capture probability for capture event <i>i</i> for month <i>i</i>
μ <sub>θ</sub>	Mean of hyperdistribution for logit capture probability
σ <sub>θ</sub>	Standard deviation of hyperdistribution for logit capture probability
$\mu_{\phi}$	Mean of hyperdistribution for log density
$\sigma_{\phi}$	Standard deviation of hyperdistribution for log density
β1 <sub>θ</sub>	Area effect on capture probability
$\beta 1_{\phi}$	Percent pool effect on fish density
	Derived Variables
$N_i$	Abundance for site <i>i</i>
$\mathbf{D}_i$	Density for site <i>i</i>
$logit(\theta_{j,i})$	Transformed hyperparameter for capture probability for site $i$ and capture event $j$ for the mark-recapture model.
$U_{2,i}$	Unmarked fish for capture event two for site <i>i</i>
	Indices
i	Index for site
j	Index for capture event (1 or 2)

# Table A.1.Definition of variables in the hierarchical Bayesian model used to<br/>estimate density of juvenile coho salmon in tributaries of the North<br/>Thompson River, British Columbia

Equation	Equation number
<b>Observation Model</b>	
$\mathbf{r}_{2,i} \sim \operatorname{dpois}(\mathbf{R}_{1,i}, \Theta_{2,i})$	A.1
$u_{1,i} \sim dpois(N_i, \Theta_{1,i})$	A.2
$u_{2,i} \sim dpois(U_{2,i}, \Theta_{2,i})$	A.3
$\mathbf{U}_{2,I} = \mathbf{N}_i - \mathbf{R}_{1,i}$	A.4
$Logit(\Theta_{i,j}) = \mu_{\Theta} + \beta o_{j,i} + \beta 1_{\Theta} X 1_i$	A.5
$\beta_{0j,i} \sim dnorm(0, \sigma_{\Theta})$	A.6
Process Model	
$D_i = \exp(\mu_{\phi} + \lambda_i + \beta 1_{\phi} \mathbf{X} 2_i)$	A.7
$\log(\lambda_i) \sim \operatorname{dnorm}(0, \sigma_{\phi})$	A.8
$N_i = D_i A_i$	A.9
Priors and Transformations	
$\mu_{\Theta} \sim dnorm(0, 0.001)$	
$\sigma_{\Theta} \sim \text{dunif}(0.01, 10)$	
$\beta 1_{\Theta} \sim dnorm(0, \sigma_{\Theta})$	
$\mu_{\phi} \sim dnorm(0, 0.001)$	
$\sigma_{\phi} \sim dunif(0.01, 10)$	
$\beta 1_{\phi} \sim dnorm(0, \sigma_{\phi})$	

Table A.2.Equations of the hierarchical Bayesian model used to estimate<br/>densities of juvenile coho salmon . See Table A.1 for the definitions of<br/>model parameters, variables, and subscripts

## **Among-Site Variation**

	Mass	ATU	P:R ratio	Ę	Gradient	LWD (pieces/area)	Latitude	Elevation (ft)	Date	Density	
Mass	1.00	-0.13			0.25	0.05	0.13	0,05		-0.24	
ATU		1.00	-0.24			-0.41	-0.37	-0.65			- 0.8
P:R ratio		-0.24	1.00		-0.66	0.49	0.56	0.68	-0.41	0.44	- 0.6
TP		0.10		1.00		0.01	-0.56	-0.41	0.62	0.21	- 0.4
Gradient	0.25	-0.08	-0.66	-0.08	1.00	-0.16	-0.13	-0.28		-0.79	- 0.2
LWD (pieces/area)		-0.41	0.49	0.01		1.00	0.21	0.58	-0:05	0.22	- 0
Latitude		-0.37	0.56	-0.56		0.21	1.00	0.70	-0.93	-0.22	0.2
Elevation (ft)		-0.65	0.68	-0.41	-0.28	0.58	0.70	1.00	-0.54		0.4
Date		0.14	-0.41	0.62		×0.05	-0.93	-0.54	1.00	0.22	0.6
Density	-0.24	0.10	0.44	0.21	-0.79	0.22	-0.22	0.13	0.22	1.00	0.8
											1

Figure A.2. Correlation matrix of all considered habitat variables in the North Thompson sites in September 2020. Positive correlations are shown in blue and negative correlations in red. Color intensity and the number (Pearson's correlation coefficient) indicate the degree of correlation. Given the threshold of 0.80, Latitude and Date were removed from the global model.

Table A.3.Site-level metrics used to relate juvenile coho salmon condition to<br/>habitat variables (temperature, physical habitat structure, water<br/>chemistry in the North Thompson River, British Columbia. Shown<br/>are the mean, range, and standard deviation among study sites (n=13).

Metric	Mean	Range	Standard Deviation	n
Latitude	51.59	(50.88 - 52.48)	0.47	13
Elevation (ft)	1,845.69	(1259 - 2752)	428.42	13
ATUS (Accumulated Thermal Units)	337.95.39	(297.12 - 386.11)	30.23	13
ADM (Average Daily Maximum °C)	11.79	(10.12 - 13.78)	1.2	13
September Mean Temperature (°C)	10.88	(9.58 - 12.44)	0.99	13
Min September Temperature (°C)	8.03	(6.57 - 9.77)	0.91	13
Max September Temperature (°C)	13.61	(11.04 - 15.95)	1.55	13
Pool-Riffle Ratio	0.61	(0.05 - 1)	0.36	13
LW Volume by Area (m <sup>3</sup> )	0.14	(0.01 - 0.89)	0.23	13
LW pieces by Area (m <sup>3</sup> )	0.36	(0.02 - 1.05)	0.33	13
Gradient (%)	1.76	(0.21 - 4.3)	1.49	13
Total Phosphorus Concentration (µg/L)	5.30	(0.75 - 12.88)	3.3	12*

\*Note that one site (Fish Trap) is excluded from Total Phosphorus, as it was not sampled at this site.

Table A.4.Mean and standard deviation for morphometric measurements and<br/>direct and indirect condition indices lipid, relative condition factor<br/> $(K_n)$ , and energy density (ED) measured from the 13 sites. The<br/>samples used for lipid and  $K_n$  analysis are noted by n, with the<br/>samples used for energy density analysis noted in brackets.

Site	n	Mass (g)	Fork Length (mm)	Lipid (% gg <sup>-1</sup> weight)	Relative Condition Factor ( <i>K<sub>n</sub></i> )	Energy Density (kJg <sup>-1</sup> )
Albreda	30 (24)	$4.17\pm0.4$	$73.5\pm2.69$	$4.17\pm0.26$	$0.89\pm0.01$	$5.78\pm0.12$
Cook	21 (15)	$7.95 \pm 1.11$	$85.38\pm5.45$	$6.01\pm0.56$	$0.96\pm0.02$	$6.91\pm0.17$
Cedar	31 (24)	$4.06\pm0.48$	$70.74\pm2.99$	$4.17\pm0.27$	$0.92\pm0.01$	$5.84\pm0.12$
Tum Tum	23 (21)	$3.68\pm0.43$	$70.83\pm2.61$	$3.78\pm0.28$	$0.9\pm0.02$	$5.51\pm0.13$
Shannon	29 (17)	$3.44\pm0.52$	$66.34\pm3.2$	$3.11\pm0.31$	$0.91\pm0.01$	$5.66\pm0.19$
Reg Christie	26 (23)	$4.38\pm0.57$	$73.54\pm2.62$	$3.81\pm0.25$	$0.94\pm0.01$	$5.6\pm0.12$
Chuck	13 (10)	$3.16\pm0.42$	$66.62\pm2.56$	$3.66\pm0.3$	$0.94\pm0.02$	$5.55\pm0.12$
Lemieux	31 (24)	$3.27\pm0.3$	$68.16 \pm 1.97$	$3.46\pm0.28$	$0.91\pm0.01$	$5.82\pm0.14$
Fennell	35 (19)	$3.08\pm0.38$	$65.8 \pm 2.38$	$2.57\pm0.28$	$0.88\pm0.01$	$5.3\pm0.15$
Haggard	25 (23)	$4.3\pm0.43$	$73.04\pm2.34$	$3.91\pm0.27$	$0.98\pm0.01$	$5.8\pm0.1$
Louis	46 (43)	$3.32\pm0.33$	$67.17\pm2.02$	$4.49\pm0.25$	$0.91\pm0.01$	$5.83\pm0.1$
Fish Trap	24 (21)	$4.16\pm0.31$	$73.96 \pm 1.63$	$4.23\pm0.3$	$0.95\pm0.01$	$5.68\pm0.19$
Jamieson	20 (19)	$5.09\pm0.25$	$79.45 \pm 1.17$	$4.21\pm0.31$	$0.96\pm0.01$	$5.86\pm0.14$



Figure A.3. Comparison between the size distribution of mass from markrecapture fish and physiology fish used for condition analyses to show the range of sizes from the overall population covered by the physiology samples. Blue indicates mark-recapture samples and purple show physiology samples.

	Condition Metric	Candidate Lipid Model	df	logLik	ΔAICc	Wi
A)	Lipid	Lipid ~ Age + LW + ATU + Mass Age:Mass	+ 8	1,137.99	0.00	0.34
	Lipid	Lipid ~ Density + Age + LW + ATU Mass + Age:Mass	J + 9	1,138.51	1.08	0.20
	Lipid	Lipid ~ Age + LW + P:R ratio + A7 + Mass + Age:Mass	ГU 9	1,138.40	1.29	0.18
	Lipid	Lipid ~ Age + ATU + Mass + Age:Mass	7	1,136.03	1.84	0.14
	Lipid	Lipid ~ Elevation + Age + LW + A + Mass + Age:Mass	ГU 9	1,138.12	1.86	0.14
B)	$K_n$	Kn ~ Age + Gradient + LW + Mass Age:Mass	s + 8	552.29	0.00	0.55
	$K_n$	Kn ~ Density + Age + Gradient + L + Mass + Age:Mass	.W 9	552.50	1.69	0.24
	$K_n$	$Kn \sim Age + Gradient + LW + ATU$ Mass + Age:Mass	<sup>(+</sup> 9	552.42	1.85	0.22
C)	Energy Density	$ED \sim Age + Mass + TP + Age:Mas$	ss 7	-146.65	0.00	0.12
	Energy Density	$ED \sim Age + ATU + Mass + TP + Age:Mass$	8	-145.60	0.03	0.12
	Energy Density	$ED \sim Age + LW + ATU + Mass + T$ Age:Mass	P + 9	-144.71	0.40	0.10
	Energy Density	$ED \sim Age + Mass + Age:Mass$	6	-148.22	1.02	0.07
	Energy Density	ED ~ Date + Age + Mass + TP + Age:Mass	8	-146.31	1.45	0.06
	Energy Density	$ED \sim Age + Lat + Mass + TP + Age:Mass$	8	-146.33	1.48	0.06
	Energy Density	$ED \sim Date + Age + ATU + Mass + Age:Mass$	TP 9	-145.36	1.70	0.05
	Energy Density	ED ~ Age + Gradient + Mass + TP Age:Mass	8 +	-146.48	1.79	0.05
	Energy Density	$ED \sim Date + Age + LW + ATU + M$ + TP + Age:Mass	lass 10	-144.34	1.81	0.05
	Energy Density	ED ~ Age + ATU + Mass + Age:Ma	ass 7	-147.56	1.83	0.05
	Energy Density	ED ~ Elevation + Age + Mass + TF Age:Mass	<b>P</b> + 8	-146.50	1.83	0.05

Table A.5.Models in the  $\triangle AICc < 2$  model set relating juvenile mass and site<br/>environmental and habitat variables to condition metric A) whole-<br/>body lipid, B) energy density, and C) Relative Condition ( $K_n$ ).

 <b>Condition</b>	Candidate Lipid Model	df	logLik	ΔAICc	w <sub>i</sub>
Energy Density	ED ~ Age + LW + P:R ratio + ATU + Mass + TP + Age:Mass	10	-144.35	1.84	0.05
Energy Density	$ED \sim Elevation + Age + ATU + Mass $ + TP + Age:Mass	9	-145.47	1.92	0.05
Energy Density	$ED \sim Age + LW + Mass + TP + Age:Mass$	8	-146.55	1.93	0.05
Energy Density	$ED \sim Age + P:R ratio + Mass + TP + Age:Mass$	8	-146.58	1.98	0.04
Energy Density	ED ~ Density + Age + Mass + TP + Age:Mass	8	-146.59	2.00	0.04

 $\Delta$ AICc is the difference between model *I* and the best model of all considered, *df* are the degrees of freedom, logLik is the log likelihood of the model, and *w<sub>i</sub>* is the Akaike weight, or the probability of the model being the best model in the set. All models included mass, age and a mass-age interaction as fixed factors, and a random intercept by site.



Figure A.4. Correlation of condition metrics. R and p-values are shown in the plot, R indicating the proportion of variance in the y-axis condition metric explained by x-axis condition metric, while the p-value demonstrates the correlation between the variables (Pearson's correlation coefficient)

### **Seasonal Variation**

Table A.6.Pairwise comparisons between months across sites for repeat<br/>sampling for slopes and intercepts from the base regression model<br/>with month and mass. P-values of protein and all condition metrics<br/>are reported. Asterisks highlight significant differences (p-value <<br/>0.001 =\*\*\*, p-value < 0.01 =\*\*, p-value < 0.05=\*)</th>

		Lipid		Protein		K <sub>n</sub>		ED	
Stream	Contrast	Intercept p-Value	Slope p- Value	Intercept p-Value	tSlope p-Value	Intercept ep-Value	Slope p- Value	Intercept p-Value	Slope p- Value
Cedar	April - July	2.305e- 24***	1.000	0.278	0.692	1.328e- 08***	1.000	3.898e- 11***	1.000
Cedar	April - August	5.975e- 17***	1.000	0.002**	0.953	6.252e- 09***	1.000	1.742e- 10***	1.000

		Lipid		Protein		K <sub>n</sub>		ED	
Stream	Contrast	Intercept p-Value	Slope p- Value	Intercep p-Value	tSlope p-Value	Intercept ep-Value	Slope p- Value	Intercept p-Value	Slope p- Value
Cedar	April - September	9.888e- r 08***	0.001**	0.082	1.000	2.336e- 06***	1.000	6.246e- 07***	0.276
Cedar	July - August	0.466	1.000	0.537	0.014*	1.000	1.000	1.000	1.000
Cedar	July - September	1.441e- r 05***	0.089	1.000	1.000	1.000	0.833	0.058	0.166
Cedar	August - September	r 0.020*	0.071	1.000	0.033*	0.634	1.000	0.234	1.000
Reg Christie	April - July	3.356e- 24***	0.004**	0.596	1.000	2.116e- 08***	1.000	3.526e- 09***	0.012*
Reg Christie	April - August	2.567e- 06***	0.268	6.670e- 04***	1.000	2.404e- 06***	2.262e- 05***	1.499e- 05***	0.036*
Reg Christie	April - September	r 0.192	1.411e- 06***	0.021*	1.000	2.578e- 04***	1.000	0.003**	2.000e 04***
Reg Christie	July - August	6.288e- 07***	0.925	0.326	1.000	1.000	0.366	0.015*	1.000
Reg Christie	July - September	9.929e- r 16***	1.000	1.000	1.000	0.035*	1.000	8.619e- 06***	1.000
Reg Christie	August - September	r 0.020*	1.000	0.927	1.000	0.854	1.166e- 04***	0.123	1.000
Tum Tum	July - August	5.618e- 05***	1.000	0.013*	1.000	1.557e- 05***	1.000	0.015*	1.000
Tum Tum	July - September	1.992e- r 06***	0.820	1.000	0.027*	8.177e- 04***	1.000	1.224e- 04***	0.898
Tum Tum	August - September	r 1.000	1.000	0.004**	0.005**	0.614	1.000	0.319	0.571



Figure A.5. Raw data points for each condition metric and percentage protein plotted out with modelled slopes across months for A) Cedar, B) Tum Tum and C) Reg Christie. Regression lines are derived from the base model determining condition from the base model of mass with a month interaction for each site. The dashed red horizontal line represents the hypothesized condition threshold between storage and structural energy, helping denote the probable surplus energy available in individuals (2 % lipid, 1.0 K<sub>n</sub>, and 4.5 kJ/g ED).