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Associations between stream habitat and energetic condition in juvenile coho salmon (*Oncorhynchus kisutch*)

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Abstract

Spatiotemporal variation in habitat quality and quantity impacts individual fish energetics by influencing growth, energy storage, and survival, ultimately shaping population dynamics. However, few studies have explicitly linked individual energetic condition to habitat variation across both space and time. In two studies, we investigated the influence of variation in freshwater habitat characteristics (September 2020) and season (July 2022 to April 2023) on both physiological (e.g., percent lipid, percent protein, and energy density) and morphological (e.g., relative condition factor) metrics of juvenile coho salmon energetic condition in interior British Columbia, Canada. Physiological metrics were associated with spatial and temporal variation in habitat. Among sites, higher percent lipid was associated with lower water temperature and higher energy density with elevated stream nutrient concentrations. Across seasons, energetic condition declined over both summer and winter. Post-winter percent lipid and energy density values converged on proposed survival thresholds. Collectively, this research demonstrates the utility of physiological energetic condition metrics as tools for quantifying how habitat changes affect juvenile salmon energetic condition, improving evaluations of habitat protection and restoration actions.

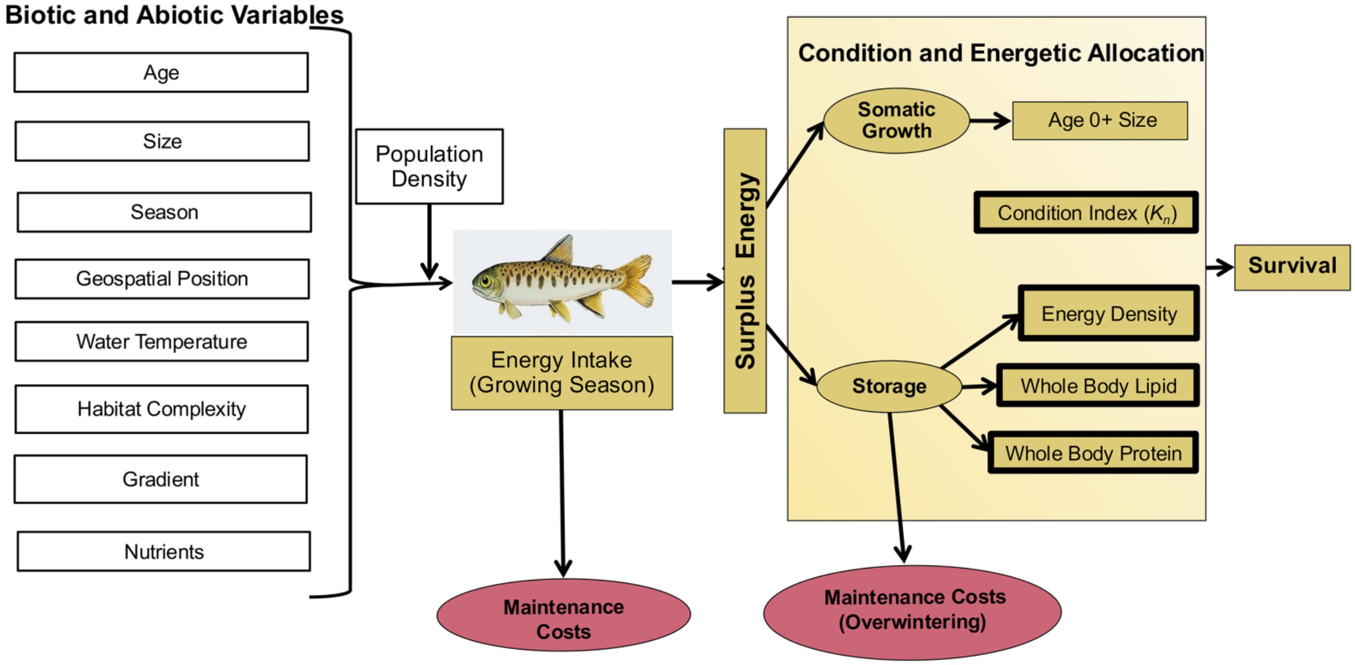
Key words: fish habitat, conservation physiology, energetic status, juvenile salmon, lipid

Introduction

Energetic condition in fish is linked to survival (Wilson et al. 2021) and thus can be an important indicator of population-level change (Stevenson and Woods 2006). Individual energetic condition is defined by the somatic composition and total energy reserves, which can be represented by various physiological and biological indices (Cooke et al. 2013; Mallett et al. 2024). Fish face several abiotic and biotic constraints on their energy balance; therefore, energetic condition is influenced by various factors like physical habitat composition, ecosystem processes, and competition for resources (Fausch 1984; Rossi et al. 2024). After meeting the demands of essential metabolic processes, individual fish allocate surplus energy to growth and/or energy storage (Brett et al. 1969; Post and Parkinson 2001), which are often correlated with survival (Quinn and Peterson 1996; Giacomini and Shuter 2013). An individual's energetic condition, and subsequently survival, may therefore reflect the combined effects of population density, physical habitat, and essential biological processes (e.g., metabolic rate) (Bolger and Connolly 1989; Stevenson and Woods 2006) (Fig. 1). Understanding individual-level energetic responses to habitat variation clarifies the mechanistic pathways between habitat and population changes, and thus could improve ability to predict population-level outcomes (Patterson et al. 2016; Mallett et al. 2024).

Fish energetic condition may be influenced by a suite of key habitat features, often through complex interactions (Beckman et al. 2000; Crozier et al. 2008). Salmonids are particularly sensitive to their freshwater rearing habitat, with variation in habitat features linked to individual energetic condition (Fig. 1). Increased fish density can have strong impacts on intraspecific competition and habitat selection, influencing energy intake from the surrounding habitat and ultimately affecting energetic condition (Grossman and Simon 2020). Water temperature and other habitat conditions (e.g., primary productivity) can be key drivers of size and energetic condition at early life stages (Railsback 2022; Kiffney et al. 2025). For instance, rearing temperatures above the optimum range (i.e., 12–16 °C) for long periods (Richter and Kolmes 2005) may cause decreased juvenile salmonid energetic condition, evidenced by decreased growth (Marine and Cech 2004), increased predation vulnerability, reduced swimming performance (McInturf et al. 2022), and lower energy stores (Feldhaus et al. 2010; McMillan et al. 2012). Temperature also interacts with food availability by influencing ener-

Fig. 1. Diagram of hypothesized linkages between 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) influences both the energy available for intake and the energetic costs, determining an individual's metabolic requirements and energetic allocation strategies for surplus energy, which may influence survival. Population density acts as a mediator for the other variables, influencing the absolute energy intake for a given individual. Red ovals represent energy subtracted due to waste and metabolic maintenance costs required for survival, while yellow ovals indicate possible allocation of energy towards either growth or storage. Condition metrics used in this study to identify energetic condition and energetic allocation are indicated in the bolded yellow boxes.



getic requirements, food-seeking behaviour, and even digestion and processing (Brett et al. 1969; Volkoff and Rønnestad 2020). As metabolic rate rises with temperature, fish must increase food intake to meet higher metabolic and energetic demands, further linking temperature and habitat productivity to energetic condition (Lusardi et al. 2020; Iino et al. 2022). Other habitat features like higher latitudes and elevation (Finstad et al. 2009; Berg et al. 2011), gradient (Bryant et al. 2004), and physical habitat structure (e.g., hydraulic habitat composition, large wood (LW), and substrate) (Naman et al. 2018) modulate energy available to an individual fish, which affects biological factors like body size (Post and Parkinson 2001), behaviour, and life history strategy (e.g., migration timing) (Morgan et al. 2002).

Seasonal variation in habitat factors can affect both energetic availability and costs in juvenile fish (Beerens et al. 2015), resulting in shifts in energy use towards storage or growth based on survival requirements (Biro et al. 2004; Hurst 2007; Mogensen and Post 2012; Birnie-Gauvin et al. 2021). During the growing season, predation risk may drive energy allocation towards growth to reduce predator vulnerability (Sogard 1997), whereas juveniles may prioritize energy dense lipid stores before winter when the risk of starvation increases (Post and Parkinson 2001; Giacomini and Shuter 2013). Documenting seasonal changes in energetic condition would improve our understanding of juvenile energetic allocation strategies that could influence future survival.

Despite extensive studies comparing habitat or season to proxy measures of juvenile fish condition (e.g., behaviour or body size) and studies measuring energetic condition directly, few field-based studies have explicitly linked these approaches by quantifying how seasonal and among-site variation in habitat features influences individual energetic condition (Biro et al. 2021). Other studies have used theoretical models or laboratory experiments to predict energetic condition responses based on variation in specific habitat features (e.g., temperature or food availability), but lack field validation (e.g., Mogensen and Post 2012; Wilson et al. 2021). Field studies assessing individual energetic condition in relation to measured habitat variation could help clarify these complex relationships.

Energy stores can be approximated by various physiological (e.g., lipid, protein, and energy density (ED) and morphometric measurements (e.g., Le Cren's relative condition factor, K_n), which can be used as surrogates of overall energetic condition (Wuenschel et al. 2018). As the main energetic constituents of fish, lipid and protein proportions reflect energy storage and growth and are linked to juvenile salmonid survival, while ED integrates total energetic reserves across tissues (Weber et al. 2003; Næsje et al. 2006; Wilson et al. 2021). K_n provides a noninvasive, mass-independent proxy for energetic status within populations by standardizing individual mass relative to expected mass at a given length, thus accounting for allometric growth and removing the direct effect of body size (Brosset et al. 2023). Together, these metrics capture complementary aspects of energetic condition; however, their mechanistic response to spatial and temporal variation in habitat remains poorly resolved.

Here, we examined associations between freshwater habitat and juvenile coho salmon (*Oncorhynchus kisutch*) energetic condition in several British Columbia streams. We addressed this goal with two complementary approaches: (1) A spatial study measuring energetic condition relative to different rearing habitats defined by factors including temperature, nutrients, gradient, elevation, rearing density, and physical habitat composition (see Table 1) and (2) a temporal study evaluating whether seasonal changes in habitat were associated with a shift in energetic condition in response to changing energetic availability or demands. Individual energetic condition was measured using four metrics: whole-body lipid (percent lipid), whole-body protein (percent protein), Le Cren's relative condition factor (K_n), and ED. We used multi-level models (spatial study) and linear regressions (temporal study) to describe linkages between individual and habitat-level variables and energetic condition. The results from these analyses reveal linkages between individual energetic condition and spatial and temporal variation in habitat. In addition, our findings demonstrate how relatively small changes in habitat metrics can measurably change individual energetic condition and in some cases approach predefined energetic thresholds of salmon survival.

Materials and methods

Experimental design

Study area

We sampled 13 small coho salmon streams off the mainstem (referred to as sites throughout) in the North Thompson watershed (Fig. 2) of British Columbia, Canada. The North Thompson is a snowmelt-dominated watershed with streams experiencing high spring flows from snowmelt (freshet), and low flows both during dry, hot summer and autumn conditions, and in winter when precipitation accumulates as snow (Déry et al. 2012). The North Thompson watershed features diverse physical stream habitats and a climate gradient from northern streams with long, cold winters to southern streams with warmer summers and winters. Anthropogenic impacts in the watershed include historical and current forestry activity, linear development, mining, and residential and agricultural land use (Bradford and Irvine 2000).

Focal species

This study focused on juvenile coho salmon from the North Thompson Conservation Unit (Arbeider et al. 2020), a genetically distinct group included in the Interior Fraser River Coho (IFC) salmon Designatable Unit (COSEWIC 2016). The IFC is designated by the Committee on the Status of Endangered Wildlife in Canada as Threatened due to declines in marine survival and threats to their freshwater habitat, including drought, increased water temperatures, and urbanization (COSEWIC 2016; Arbeider et al. 2020). Only wild coho salmon are present in our study sites. Coho salmon adults spawn in the fall and early winter and fry emerge from the gravel in the spring between March and July to begin exogeneous feeding. Juvenile coho salmon then spend 1–2 years in fresh water, rearing in natal streams, wetlands, side channels, and the mainstem before migrating to the ocean as Age 1+ or 2+ smolts in the spring (Arbeider et al. 2020; Milner et al. 2025). Most coho salmon spend 18 months in the ocean before returning to freshwater to spawn (Groot and Margolis 1991).

Fish sampling

We conducted studies to explore (1) spatial variation in juvenile coho salmon energetic condition among 13 sites, and (2) temporal variation in energetic condition across a 10-month period using a subset of three focal sites (Table S.1). For the spatial variation study, juvenile coho salmon were sampled once at all 13 sites between 20 September and 1 October in 2020 for physiological samples and to estimate density. Fish captured were from two cohort years, predominantly young-of-the-year (Age 0+) juveniles, and a smaller number of parr that emerged the previous year (Age 1+). Individual fish collected in 2020 were aged via visual inspection of scale circuli counts (Milner et al. 2025). Three of the 13 sites were repeatedly sampled for the temporal study in July, August, and September 2022, and again in April 2023. Fish from Tumtum Creek in April 2023 were not included due to an unexpected release of fish from a nearby system from fish salvage operations during pipeline construction that would have confounded our results for that sampling event.

For each fish sampling event and site, up to 40 baited minnow (Gee) traps with 1/8″ mesh were distributed in a designated area, or reach (established by Cunningham et al. 2023) to estimate density. Briefly, a stream reach is defined as the surveyed area selected at each site for its accessibility, potential for juvenile coho salmon rearing habitat, and placement within or downstream of known coho salmon spawning reaches (wetted area < 1676 m^2). Physiology samples were taken by trapping just outside of the focal reaches (above and/or below) to reduce the impact of fish removals on the concurrent density study within the focal reach (Table S.1). Prior work in the region had indicated that the trapping methods were not size-selective across the typical size range of Age 0+ and Age 1+ juveniles (Braun, unpublished data, 2025; Milner et al. 2025). All fish were measured for fork length and weight to the nearest 1 mm and 0.1 g, respectively, in the field.

Fish densities

Detailed mark–recapture methods are provided in the Supplementary material (Mark–Recapture, Fish Density) and outlined in Milner et al. (2025). Briefly, juvenile coho salmon densities were estimated with a hierarchical Bayesian closed mark–recapture model (Fig. S.1; Tables S.2 and S.3) with data collected in September from 2019 to 2023 using minnow trapping and visible implant elastomer tags (Northwest Marine Technologies, Shaw Island, WA). All fish sampling fol-

Table 1. Hypotheses for the potential influence of individual fish metrics and spatial and temporal habitat variables on salmon condition metrics: percent lipid, energy density (ED), and relative condition factor (K_n).

Explanatory variables	Description of explanatory variable	Predicted impact on salmon condition	Direction	References
Individual fish-level				
Fish density	Estimated juvenile coho density (fish·m^{-2})	Increased fish density will decrease individual fish energetic condition.	Negative	(Rosenfeld et al. 2005; Utz and Hartman 2009; Vincenzi et al. 2012; Grossman and Simon 2020; Matte et al. 2021; Hasegawa et al. 2024)
Age	Fish age (0+/1+)	Energetic condition is higher for an Age 1+ fish compared to an Age 0+ fish of the same mass.	Positive	(Post and Parkinson 2001; Jonsson and Jonsson 2003; Biro et al. 2005; Ebersole et al. 2006)
Size	Whole-body mass (g)	A positive allometric relationship between size (length or mass) and condition, with larger juveniles having highest condition.	Positive	(Post and Parkinson 2001; Hurst and Conover 2003; Biro et al.2004, 2005)
Habitat site-level				
Season	Month (April (spring), July/August (summer), or September (fall)	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 (i.e., preparation for overwintering energetic storage).	Positive (April–September), negative (September–April)	(Post and Parkinson 2001; Hurst and Conover 2003; Cleary et al. 2012; Mogensen and Post 2012; Biro et al. 2021; Spangenberg et al. 2023)
			Higher across-season sensitivity in lipid and ED, less in K_n	
Geospatial location	Elevation and latitude	Higher elevations and latitudes with shorter growing seasons will lead to cumulatively longer periods of net energy deficits (*i.e.*, overwintering). Fish at lower elevation and latitudes sites will direct relatively less energy to storage and show lower seasonal variation, due to differing overwinter energetic storage requirements to stay above the minimum energetic survival threshold.	Positive	(Yamahira and Conover 2002; Biro et al. 2004; Parra et al. 2009; Berg et al. 2011; Gallagher et al. 2022)
Water temperature	Accumulated thermal units (ATUs)	Increased temperatures can increase primary productivity and energy intake but at temperatures above a physiological threshold can also decrease energetic condition by increasing metabolic costs to individual fish and causing physiological stress.	Positive (up to a threshold), negative past the threshold	(Lusardi et al. 2020; Volkoff and Rønnestad 2020; Armstrong et al. 2021; Araújo et al. 2023)
Habitat complexity	Large wood pieces by total area (m^{-2}), pool:riffle ratio	Increased habitat complexity will provide higher quality habitat, potentially through improved food availability and energetic refuge.	Positive	(Bisson et al. 1988; Fausch and Northcote 1992; Ebersole et al. 2009; Mellina and Hinch 2009; Jorgensen et al. 2021)
Gradient	Gradient (percentage)	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	(Beechie and Sibley 1997; Bryant et al. 2004)
Nutrients	Dissolved total phosphorus (µg·L^{-1})	Higher nutrients can indicate 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	(Kiffney et al. 2014; Lapointe and Rasmussen 2016)

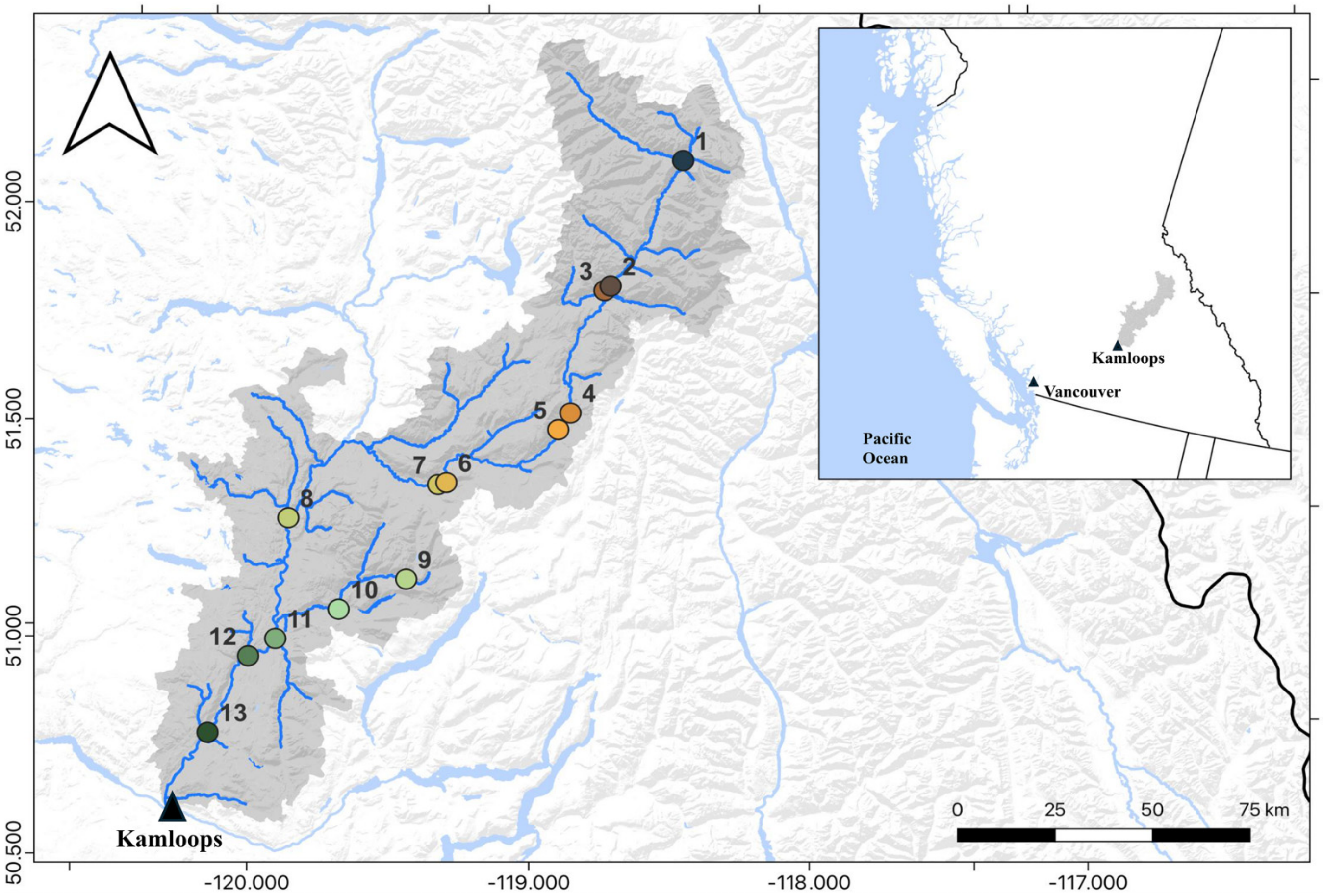
Note: Direction of the predicted effect is noted (positive or negative).

lowed the protocols outlined in Animal Use Protocols #21-010 and #22-006 approved by the DFO Pacific Region Animal Care Committee following the Canadian Council on Animal Care guidelines.

Physiology sample collection

Juvenile coho salmon were randomly sampled from the out-of-reach minnow trap catches among sites (n = 3–46; mean mass = 3.6 g, range = 0.8–16 g). Fish were euthanized

Fig. 2. Study site locations in tributaries along the North Thompson River in British Columbia. Each site is numbered and has a unique colour. 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) Barriere, (10) Haggard, (11) Louis, (12) Fishtrap, and (13) Jamieson. Site colours match Fig. 4. This map uses a Lambert equal area projection, with North American Datum 1927. Spatial files for streams, shown in blue, were provided by the Freshwater Atlas (Government of British Columbia 2019). Elevation data are from United States Geological Survey (USGS 2023). Provincial and state boundaries in black are from the North American Atlas (Government of Canda 2021).



with a lethal dose (100–200 ppm) of buffered MS-222 solution and then frozen on dry ice. Fish were transferred to a −80 °C freezer for longer-term storage. To test the assumption that the fish sizes used for physiological assays were representative of the population, we compared the fork length distribution of fish collected for physiological analysis with that of the total catch for each site (Fig. S.2). Due to a minimum size cutoff for the physiological assay used to calculate ED, smaller fish were underrepresented in the final analysis compared to their occurrence in the population.

Habitat variables

Water temperature

Water temperature is a key factor influencing salmonid overall condition and life history (Brett 1971; Volkoff and Rønnestad 2020). Water temperatures were recorded by hourly HOBO U20 or TidBit V2 loggers (Onset Computer Corporation, precision ±0.2 °C) at each site in 2020 and 2021. These loggers were either suspended in acrylonitrile butadiene styrene stilling wells attached to large boulders or to steel posts. Mean daily temperatures and mean monthly temperatures were calculated from continuous hourly data. Accumulated thermal units (ATUs) were calculated by summing daily averaged water temperatures for the 30-day period prior to fish sample collection at each site in 2020 (spatial site comparison). ATUs among the 13 sites ranged from 297 to 386 ATUs for the 30 days prior to sampling.

Nutrients

We 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 and Canfield 1991; Lewis and Ganshorn 2007). TP is an index of stream nutrient status, reflecting bottom-up controls on primary productivity and a coarse indicator of potential food availability for juvenile coho salmon. TP levels were measured at least once in 2021 and 2022 for 12 of the 13 sites (excluding Fishtrap). Samples were collected mid-water column in pre-washed 50 mL glass test tubes, transported on ice, stored at 4 °C, and analyzed at the Cultus Lake Salmon Research Laboratory following methods described in Murphy and Riley (1962). The differences in TP among sites were consistent between years. Therefore, we used the TP value at each site from either September of 2021 or 2022, or the average if both were taken in our 2020 spatial study. TP ranged from 0.75 to 12.88 $\mu g \cdot L^{-1}$.

Physical habitat characteristics

Habitat structure is important for juvenile coho salmon for energetic and predator refuges and for resource availability. See Cunningham et al. (2023) for a more detailed description of methods and data. Site reaches were measured during low flow periods in 2019 and 2020 (July–August). All larger pieces of wood (length $>$ 1.5 m and diameter $>$ 0.1 m) within the bankfull area of each channel were counted and individually measured. This measurement was then transformed into a metric of LW pieces m^{-2} by dividing the volume of LW by the bankfull area to account for the varied stream sizes across sites. Macrohabitat units were classified into pool and riffle areas, measured, and then transformed into a proportional metric of pool to riffle ratio, by dividing the pool area by the total stream 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% and 0.21% gradient and 0.05–1 pool–riffle ratio). LW was highly variable among sites and ranged from as low as 0.02 to 1.05 pieces m^2.

Seasonality

Stream habitat conditions change seasonally; therefore, we assumed fish collected from one month experienced a different suite of habitat variables compared to fish collected from other months. Month was used as a categorical variable in our temporal analysis (see below) that integrates seasonal variation in hydrology (Déry et al. 2012), photoperiod (Spangenberg et al. 2023), temperature (Moore 2006), variation in primary and secondary productivity (Dunkle et al. 2024), and other biotic factors like prey availability, competitors, and predators.

Calculating condition metrics

We determined energetic condition of individual juveniles by measuring isolated fractions of lipid, moisture, and carbon content, and then calculating for percent lipid, percent protein, and ED as in Wilson et al. (2021). Briefly, we calculated whole-body lipid weight and total percent lipid for each individual using an adaptation of the Bligh and Dyer method (Bligh and Dyer 1959). Thawed wet mass (nearest 0.001 g) measured in the laboratory and field fork length (nearest 1 mm) were used in our analyses. To calculate percent protein, we dehydrated samples to measure percent hydration and then fired to ash combustion to measure percent carbon. ED was calculated with percent lipid and protein using methods and constants used by Breck (2008). We calculated Le Cren's relative condition factor (K_n) for the juveniles in our sample using individual fork length and mass and used mark–recapture data collected in September from 2019 to 2023 to calculate the population-specific constants (Le Cren 1951). For more detail and equations, see Supplementary material (Physiology Methods).

In total, 381 juvenile coho salmon from 13 sites in 2020 were processed for the spatial study. Percent lipid was determined for 354 individuals. Protein and ED were calculated for 239 individuals using moisture and carbon concentration. For the 2022–2023 temporal study, 166 individuals from 3 sites were processed for lipid analysis (15–16 samples per site and month), with protein and ED calculated for 136 individuals. Some samples were eliminated due to inadequate tissue volume for replicates of lipid, moisture, or carbon samples, or high variance among within-individual replicates. All individuals were initially processed, and samples excluded due to high variance represented a random subset of samples across sizes and sites, making systematic bias unlikely.

Data analyses

Spatial variation in energetic condition

The objective of our spatial analysis was to describe the relationships between measured habitat variables and three condition metrics (percent lipid, relative condition factor (K_n), and ED). Protein was not selected for further analysis as it showed limited variation with low variability across sites (range between 16.7% and 18.4%, within-site CV = 3.8%–9.0%, among site CV = 2.7%). To test the hypotheses outlined in Table 1, we used a multi-level modelling approach to account for the data structure (individual- and site-level explanatory variables) (Gelman and Hill 2007; Brooks et al. 2024). For more information, see Supplementary material (Data Analyses: Spatial Model, Fig. S.3).

For each of the three condition metrics, we 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). We hypothesized that fish mass is an important predictor of condition and energetic allocation. All models included age, mass, and an age–mass interaction to account for the strong allometric relationship between mass and condition and the strong positive interaction between age and size. Top models of the candidate set for model averaging were selected using the Akaike information criteria for small sample sizes (AICc) (Burnham and Anderson 2002). We performed model averaging using the top candidate models when there was no clear top model (weights < 0.9) (Symonds and Moussalli 2011; R package *MuMin*, Bartoń 2024). We compared the model-averaged conditional coefficients for the relative influence of each variable on the condition metric (relative variable importance, or RVI). RVI was assessed by summing the AICc model weights (ω_i) for the variable across all models in the set where it was present (Burnham and Anderson 2002). Model-averaged coefficients were also used to calculate predicted condition values. Because mass was centered, the intercept and month coefficients represent the monthly average for the modelled condition of an averaged-weight fish. We evaluated the predictive performance of hierarchical models using root mean squared percentage error (RMSPE).

Seasonal variation in energetic condition

We assessed seasonal changes in juvenile coho salmon condition for Age 0+ and 1+ fish. To test the seasonal hypotheses in Table 1, we constructed a linear regression model for each condition metric at each site (Hurst and Conover 2003). We included the main effects of mass and month and their interaction as explanatory variables, centering the predictor variable (mass).

We used a Gaussian distribution for models describing K_n and ED, and a beta regression for percent lipid and protein. We included percent protein in this analysis to compare month to month variation within the same site. Percent lipid and protein were logit-transformed. Continuous predictor variables were log-transformed to improve normality and homogeneity of variance (Douma and Weedon 2019; Geissinger et al. 2022). We extracted parameter estimates to determine the monthly mean condition for an averaged-weight individual fish and the change in relationship between condition and mass across months. For further information, see Supplementary material (Data Analyses: Seasonal Model).

All statistical analysis was performed using R 2023.12.1 (R Core Team 2024), in RStudio (Posit team 2024).

Results

Spatial variation in energetic condition

Juvenile coho salmon energetic condition and rearing habitats varied among the 13 sites (Tables S.4 and S.5). Individual measures of whole-body lipid (percent lipid) ranged from 1.0 to 9.6 (%), relative condition factor (K_n) ranged from 0.78 to 1.17, and ED from 3.3 to 7.9 (kJ·g^{-1}) across all fish sampled. Within a stream, we saw large variation in condition metrics among individual fish, and even greater variation among sites (percent lipid: within site CV = 5.6%–10.9%, among site CV = 20.3%; K_n: within site CV = 0.9%–2.4%, among site CV = 3.2%; ED: within site CV = 1.7%–3.4%, among site CV = 6.5%). As expected, there were clear and consistent effects of age and mass and their interaction on all condition metrics (Fig. 3; Table S.6, Supplementary material: Spatial Model). Overall, temperature, gradient, and TP were the habitat attributes that had the largest effect on energetic condition metrics (Fig. 3), with each of these best describing a different condition metric.

Juvenile percent lipid

Juvenile coho salmon sampled from cooler streams had higher mean percent lipid than fish from warmer streams (Fig. 4C). ATU had the largest effect on percent lipid of all the habitat variables considered (Fig. 3A) and was the only habitat variable included in the top model (RMSPE = 33.8%, Table 2) and present in all models in the candidate set (RVI = 1.0). Although 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 an uncertain effect (95% confidence limits crossed 0). Comparing predicted lipid concentration in fish between the coolest and warmest sites, we estimated a decline from 3% to 1.8% (a 40% change in predicted lipid concentration) for an average-sized 0+ fish. The temperature difference between the coolest and warmest sites is roughly equal to a difference in 90 ATUs or a 3 °C difference in mean temperature between streams over 30 days.

Energy density

Juvenile coho salmon had higher ED in streams with higher TP concentrations (Fig. 4I). This proxy for nutrients had the largest effect on ED of all habitat variables considered (Fig. 3C). Based on model-averaged predictions, increasing TP by 12.13 µg·L^{-1} (from lowest to highest recorded site TP concentrations) would result in an ED increase of 0.38 kJ·g^{-1} for the average fish. In other words, the ED of an average fish would increase by 6.90% with a shift in TP from lowest to highest value measured across sites. TP had an RVI of 0.88 and was in 10 of the 12 models averaged in the ΔAICc < 2 top model set (Fig. 3C). TP was the only explanatory habitat variable included in the top model for ED and the model had an RMSPE of 7.21% (Table 2).

Relative condition factor (K_n)

Juvenile coho salmon had higher relative condition factor (K_n) in higher gradient streams compared to lower gradient streams (Fig. 4F). Gradient had the largest effect on K_n among all the habitat variables considered, the highest RVI score, and was present in all three of the ΔAICc < 2 candidate models (Table 2; Fig. 3B). However, 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 signifies that the maximum difference in gradient observed in this system would result in a marginal 3% increase in K_n.

Seasonal variation in energetic condition

Overall, fish energetic condition decreased throughout the summer, and again over winter (Fig. 5). There was a consistent trend of decreasing energetic condition from July 2022 to April 2023 (Table S.7). The largest changes were observed in average percent lipid and ED, whereas changes in relative condition factor (K_n) and percent protein were largely insignificant between monthly pairwise comparisons (Fig. 5; Table S.7). Overall, larger fish had higher relative energetic condition. As indicated by a nonsignificant mass and month interaction, this positive allometric relationship did not significantly vary between July and September (Table S.7; Fig. S.4). However, in April all fish had similar percent lipid, with no clear allometric relationship between lipid and mass (Fig. S.4).

Fish energetic condition metrics tended to be highest in July and decrease throughout the summer (between July and September). The monthly average lipid declined between July and September at all sites, a similar quantity to the overwinter decrease. Percent lipid at Cedar decreased from 5.01% to 3.77% (a change of −1.24% lipid), similar to the −1.42%

Fig. 3. 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. 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 included in all possible model combinations (age, mass, and the age–mass interaction). ATU, accumulated thermal unit; LW, large wood.

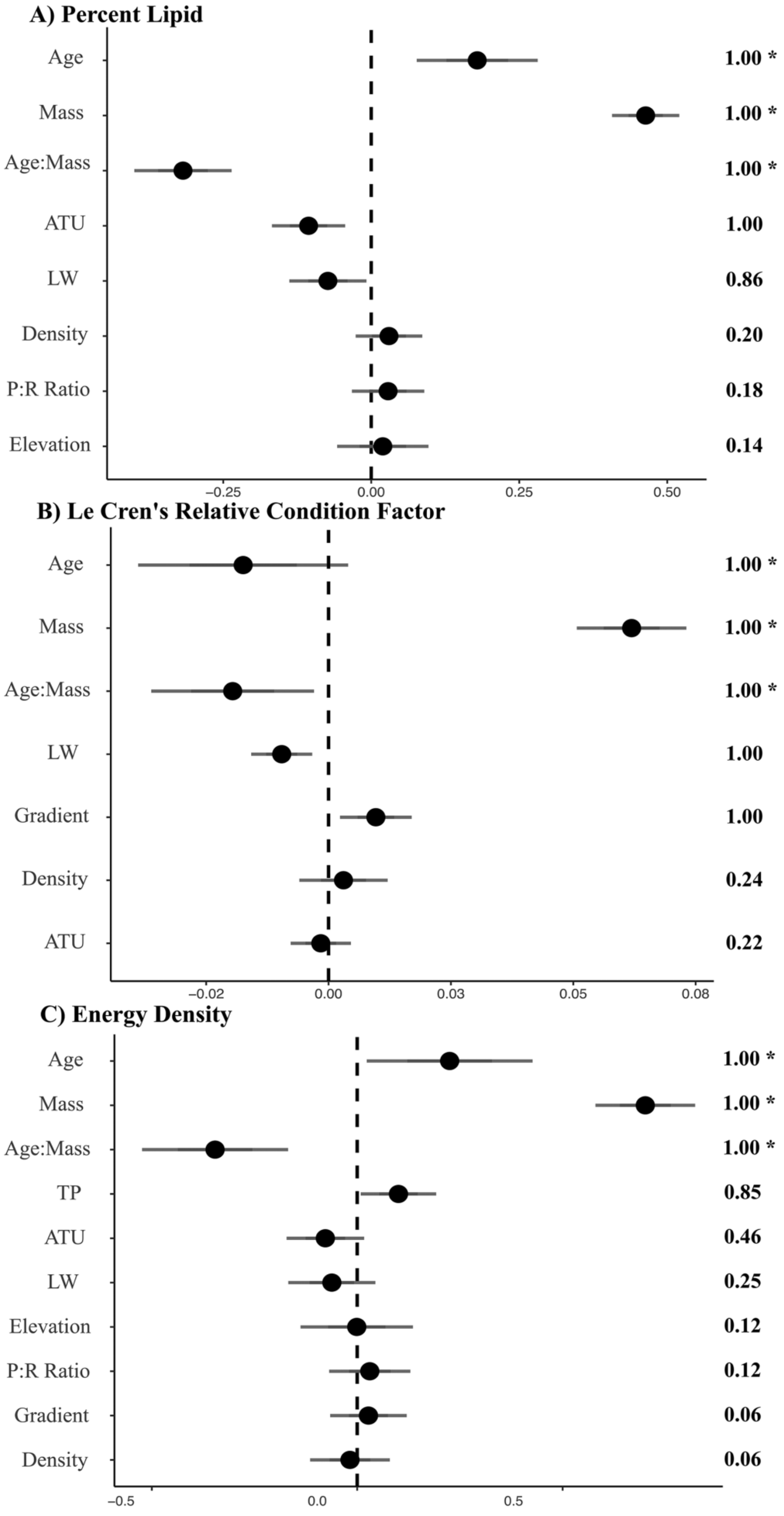


Fig. 4. The age-specific relationships between each condition metric and the significant variables from the hierarchical model. The regression line and 95% confidence area of the model-averaged coefficients are shown for each condition metric: top row: percent lipid and (A) mass, (B) large wood (LW), (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 and (H) mass, and (I) total phosphorus. Triangles, solid regression line, and lighter 95% confidence region shading represent the Age 1+ fish, while circles, dashed regression line, and darker 95% confidence region shading represent Age 0+ fish.

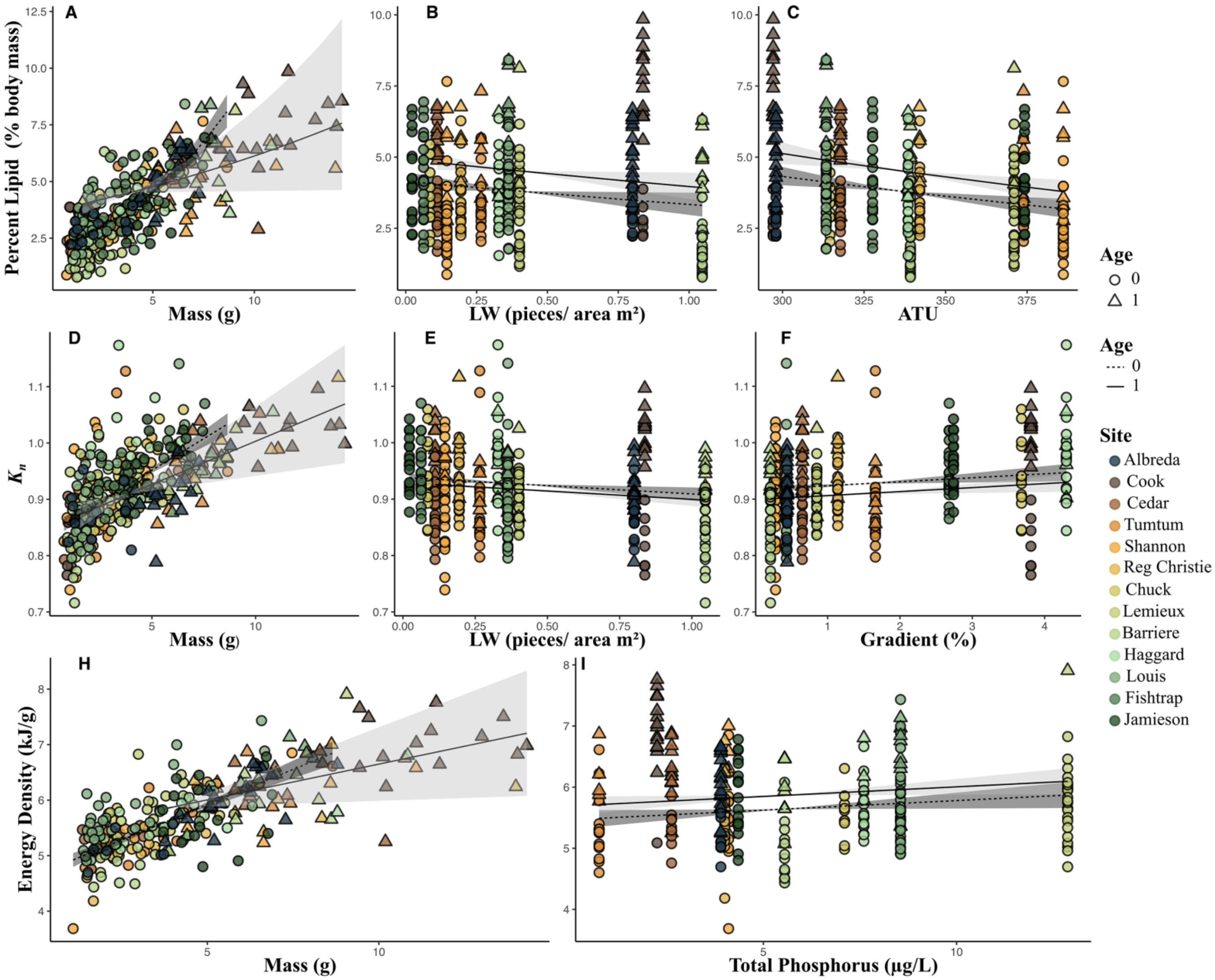


Table 2. Top models (selected as the least complex model within ΔAICc < 2) from modelling juvenile condition using three metrics.

Condition metric	Model variables	df[a]	logLik[b]	AICc[c]	ΔAICc[d]	ω_i[e]	RMSPE[f]
Percent lipid	Lipid ∼ age + ATU + mass + age:mass	7	1136.03	− 2257.73	1.84	0.14	33.78
K_n	K_n ∼ age + gradient + LW + mass + age:mass	8	552.29	− 1088.16	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

Note: Akaike information criterion (AIC) corrected for small sample size (AICc) was used to determine top model (see Table S5 for complete top model set). Note that 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. ED, energy density; TP, total phosphorus; LW, large wood.

[a] Degrees of freedom.

[b] Log likelihood.

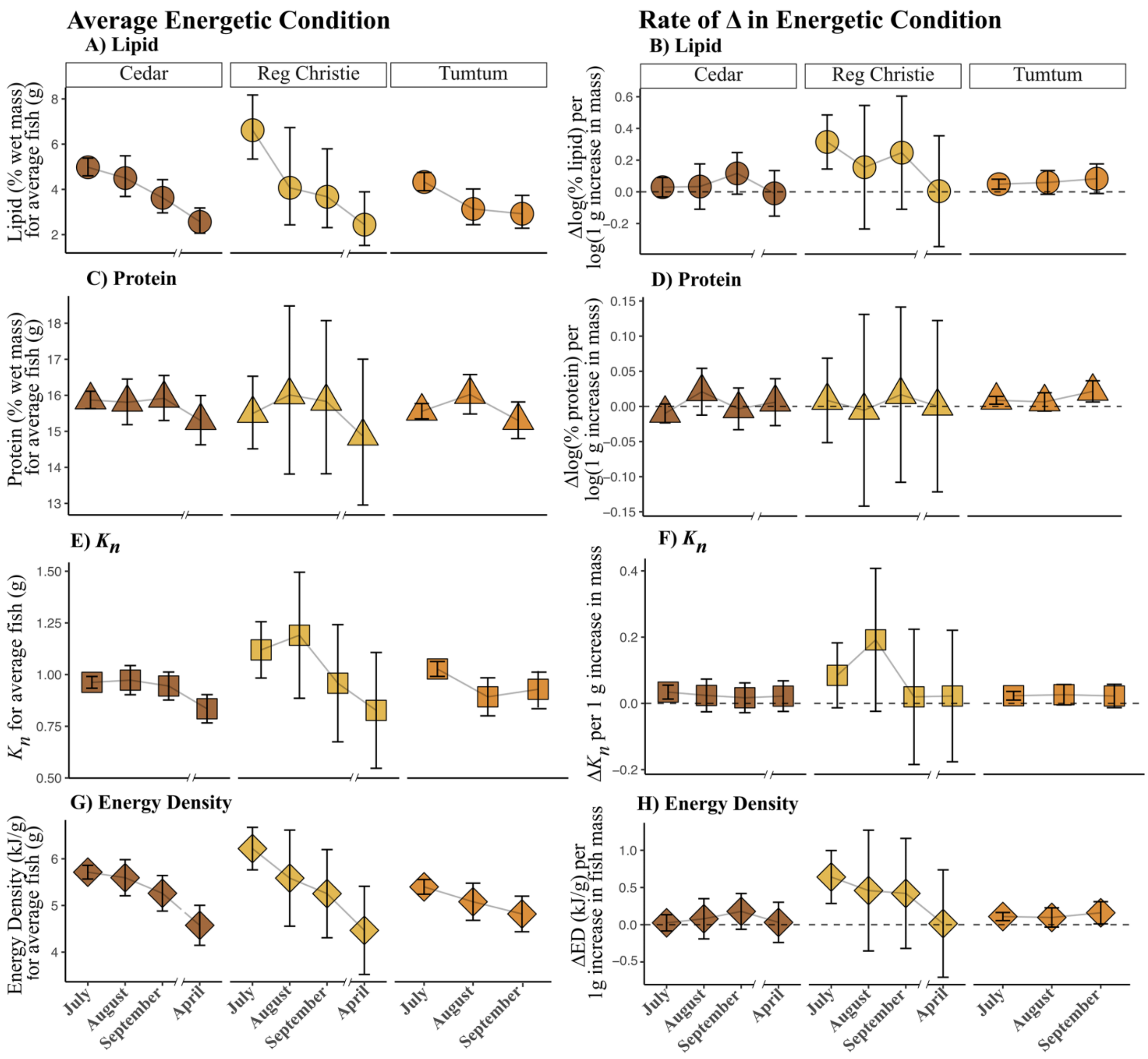
[c] AICc score of the top model.

[d] ΔAICc is the difference in AIC values between top model and the lowest AICc ranked model in the suite.

[e] ω_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.

Fig. 5. 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 Tumtum 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. S.16). The intercept plots (A, C, E, and G) represent the condition level for an average-sized fish for each month, while the slope coefficient plots (B, D, F, and H) represent the condition specific change with a 1 g increase in fish mass. The black dashed line in the slope plots represents the zero line, which indicates no relationship between condition and mass.



change at Reg Christie and −1.31% change at Tumtum (Table 3). Juvenile coho salmon ED for an average fish at all sites consistently declined throughout the summer between July and September (Cedar = −0.32 kJ·g^{-1}, Reg Christie = −0.49 kJ·g^{-1}, Tumtum = −0.56 kJ·g^{-1}) (Fig. 5G; Table 3). Relative condition factor (K_n) decreased from July to September across all sites (Cedar = −0.04; Reg Christie = −0.07, Tumtum = −0.10) (Fig. 5E). There was insignificant variance in K_n between the summer months (Table S6). The average percent protein changed marginally throughout the summer months, increasing slightly at Cedar and Reg Christie (Fig. 5C). (Cedar = 0.06%, Reg Christie = 0.32%, Tumtum = −0.15%) (Table 3).

All metrics of fish condition declined over winter between September and April. Percent lipid decreased between September and April (Cedar = −1.3%, Reg Christie = −0.7%) (Table 3) as did the variance (September CV: Cedar = 10.1%, Reg Christie = 9.1%, April CV: Cedar = 4.6%, Reg Christie = 0.4%). In April, mean percent lipid values measured 2.5 ± 0.1% at Cedar and 2.4 ± 0.1% at Reg Christie. Taken together, these results suggest that overwinter fish converged on a narrow range of percent lipid values, which may be indicative of a critical threshold for survival. Overwinter ED also declined between September and April (September–April: Cedar = −0.78 kJ·g^{-1}, Reg Christie = −0.49 kJ·g^{-1}) (Table 3). The change in average ED across different sites and

Table 3. Condition metrics 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.

Site	Month	n	Mean lipid (% gg^{-1} weight)	Mean protein (% gg^{-1} weight)	Mean K_n	Mean energy density (kJ·g^{-1})
Cedar	July	15 (15)	5.01 ± 0.16	15.82 ± 0.17	0.98 ± 0.02	5.72 ± 0.07
Cedar	August	15 (14)	4.64 ± 0.23	16.09 ± 0.12	0.99 ± 0.02	5.68 ± 0.09
Cedar	September	15 (10)	3.77 ± 0.38	15.88 ± 0.11	0.94 ± 0.02	5.40 ± 0.15
Cedar	April	15 (11)	2.52 ± 0.09	15.41 ± 0.12	0.85 ± 0.02	4.62 ± 0.06
Tumtum	July	16 (14)	4.42 ± 0.21	15.65 ± 0.12	1.04 ± 0.02	5.49 ± 0.09
Tumtum	August	15 (14)	3.54 ± 0.28	16.20 ± 0.14	0.94 ± 0.03	5.28 ± 0.11
Tumtum	September	15 (14)	3.11 ± 0.25	15.50 ± 0.18	0.94 ± 0.03	4.93 ± 0.13
Reg Christie	July	15 (12)	4.50 ± 0.21	15.36 ± 0.10	1.01 ± 0.02	5.45 ± 0.09
Reg Christie	August	15 (10)	3.38 ± 0.23	16.09 ± 0.16	0.93 ± 0.04	5.09 ± 0.12
Reg Christie	September	15 (13)	3.08 ± 0.28	15.68 ± 0.17	0.94 ± 0.01	4.96 ± 0.13
Reg Christie	April	15 (9)	2.41 ± 0.10	14.88 ± 0.24	0.81 ± 0.04	4.47 ± 0.10

Note: 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.

months revealed several significant seasonal effects between July and April, and September and April (Table S.7). We observed a consistent pattern of seasonal variation in ED across all sites, with particularly pronounced differences between summer months and April. K_n decreased from September to April at Reg Christie and Cedar (Cedar = −0.09; Reg Christie = −0.13) (Table 3), and across all sites, there were consistently significant pairwise differences in mean K_n between summer months and April. 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).

Discussion

We found that energetic condition metrics of juvenile coho salmon (percent lipid, ED, and relative condition (K_n)) were related to differences in habitat and season. Our spatial analysis showed that each energetic condition metric was associated with distinct habitat predictors; percent lipid was best predicted by temperature, ED by TP, and K_n by gradient. This suggests that these metrics may represent different aspects of individual fish condition and reflect different sensitivity to habitat variation (e.g., temperature, primary productivity, habitat complexity). Our temporal analysis revealed that energetic condition declined over winter, as expected. However, contrary to previous literature on other salmonid species (Cleary et al. 2012; Mogensen and Post 2012; Biro et al. 2021), all metrics of energetic condition also consistently decreased over summer. Taken together, our results suggest that juvenile coho energetic condition is driven by the interplay between individual physiological traits and habitat conditions.

Linking fish energetic condition with spatial habitat variation

Whole-body lipids were negatively related to water temperature, suggesting that juvenile coho rearing in warm habitats is more likely to have lower average lipids, which could translate to decreased survival (Brett 1971; Volkoff and Rønnestad 2020). Our findings align with previous studies that have demonstrated an inverse relationship between temperature and both growth and energy storage in juvenile salmonids, where colder environments tend to result in higher lipid content and larger fish size at maturity (Feldhaus et al. 2010; Ahti et al. 2020). While the inverse relationship we observed between temperature and energy storage is expected during the warmer summer months, we would expect different results during cooler times of the year, like in the spring. Furthermore, Kammerer and Heppell (2013) found that temperature was the most significant factor influencing energetic condition and growth for salmonids over their 2-year study, even more so than nutrient availability. Lower temperatures during warmer months could be a useful indicator of higher habitat quality (a set of habitat variables corresponding with higher fish energetic condition) or reflect energetic allocation strategies that promote higher lipid storage in salmonids (Berg et al. 2011).

ED was positively related to total phosphorous, suggesting that site primary/secondary productivity improves juvenile coho salmon energetic condition. This result aligns with other research demonstrating similar links between nutrient availability and fish production. For example, Lapointe and Rasmussen (2016) found that TP was a strong predictor of fish biomass in rivers and lakes across Canada, suggesting that TP can be an effective indicator of productivity. However, the effect size of TP in our analysis was small and likely reflects an indirect influence on energetic condition as TP is only a coarse proxy of resource availability for coho, which are also supported by terrestrial energy pathways (Wipfli and Baxter 2010). More direct measurements of habitat productivity like prey abundance, quality, or accessibility (Ouellet et al. 2024) may be stronger predictors of energetic condition (Saunders et al. 2018; Naman et al. 2022). Ultimately, our findings support that increased energetic condition in fish is linked to increased nutrients (indicative of habitat productivity) and that habitat productivity can be a key component in assessing habitat for juvenile coho salmon.

Interestingly, none of the energetic condition metrics were explained by juvenile coho salmon density, indicating a decoupling between individual condition and conspecific density at the spatial or temporal scale of our study. This was contrary to our hypothesis of the negative effect of density on energetic condition due to increased resource competition (Table 1). Biomass estimates (Fig. S.1) indicate that the sampled streams were at relatively high densities compared to the average coho biomass reported in Foote et al. (2025); thus, the absence of density-dependent effects could be plausibly attributed to self-thinning that may have occurred before our September sampling. While movement within the study network appeared limited during the sampling period (Braun, unpublished data, 2025; Scott et al. 1981), juvenile coho salmon may move among freshwater habitats within a stream network. Thus, a broader seasonal and interannual redistribution could decouple local density from energetic condition at individual sites (Arbeider et al. 2020; Armstrong et al. 2021).

Furthermore, measuring population density may not always reflect individual energetic condition and long-term population dynamics. For instance, the ways in which population density affects individual energetic condition can differ depending on whether the underlying habitat factors driving condition are density-dependent (e.g., competition for resources), or density-independent (e.g., temperature). The relative importance of these factors can vary substantially among species and populations (Bailey et al. 2018; Chaparro-Pedraza and de Roos 2019) as well as through time (Einum et al. 2006). Our study was not designed to tease apart this complexity. 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.

Whole-body lipid content and relative condition factor (K_n) showed weak, site-sensitive associations with lower concentrations of LW. However, this negative association was driven largely by a single site, and its removal resulted in a reversed, weakly positive effect indicating minimum biological significance. Given the uncertain effect, we did not consider this result further. Similarly, the weak positive association between K_n and gradient suggests limited biological relevance at the scale of this system. Collectively, these results indicate that while LW and gradient may be related to other important habitat variables, they are not independent drivers of energetic condition.

Fish size and age strongly constrain energetic condition and survival, with larger and older individuals generally exhibiting higher energetic reserves and survival probabilities (Brett 1965; Post and Parkinson 2001; Ahti et al. 2020). Consistent with these expectations, individual mass and age explained substantially more variation in all energetic condition metrics than habitat variables, reflecting well-established size- and age-dependent metabolic scaling and mortality risk (Brett 1964; Biro et al. 2004). However, age itself may not exert a direct effect on energetic condition. Instead, the observed patterns (including the significant age–mass interaction in our study) likely reflect the nonlinear relationship between mass and lipid storage that may vary with age (Cleary et al. 2012).

Linking fish energetic condition with seasonal habitat variation

Fish condition metrics showed contrasting seasonal patterns, with percent protein remaining stable throughout the sampled months while percent lipid and ED declined over winter. This supports previous findings that lipids are the primary constituent for energy storage (Jonsson and Jonsson 1998, 2003; Martin et al. 2017). In other overwinter studies, mortality can be attributed to significant, potentially lethal declines in energy storage in fish populations, especially for smaller and younger fish (Post and Parkinson 2001; Biro et al. 2004, 2021). Most fish sampled in this study during April approached a 2.0% lipid concentration, a threshold linked to a decline in fitness related traits and higher mortality (Simpkins et al. 2003; Wilson et al. 2021). Interestingly, April lipid concentrations appear to be independent of size, unlike the summer months where there was a strong positive allometric relationship. The change in energetic condition levels from favorable growth periods to energetically taxing stages like overwintering is a ubiquitous phenomenon previously studied in many juvenile fish species (Martin et al. 2017; Biro et al. 2021).

Contrary to our hypothesis, energetic condition also declined throughout the summer months, a typically net positive energy and growth period (Cleary et al. 2012; Mogensen and Post 2012; Biro et al. 2021). Percent lipid, ED, and relative condition were highest in July and declined through to September across all three sites, with lipid losses ranging from 1.2% to 1.3% lipid. This represents a proportional loss of approximately 24% of initial summer (July) lipid stores in these fish, which has implications for overwinter mortality. For example, low energy stores could lead to increased risk of both predation (due to aggressive foraging behaviour) and starvation (insufficient energy stores to accommodate metabolic costs as they enter the overwinter period) (Biro et al. 2021). These patterns contrast with previous observations of increasing lipid reserves from summer to autumn in temperate freshwater fish (Post and Parkinson 2001; Cleary et al. 2012; Mogensen and Post 2012), but align with the low or negative growth patterns during summer seen in juvenile coho salmon in wetland habitats of the North Thompson watershed (Milner et al. 2025), interior British Columbia coho salmon in laboratory settings (Iacarella et al. 2025) and other cold water stream salmonids in Massachusetts, USA (Letcher et al. 2025).

One plausible explanation for this unexpected decline in energetic condition over the summer is that increasing summer temperatures and possibly reduced food availability raise metabolic costs while lowering energy intake, especially in resource-limited, oligotrophic streams (Biro et al. 2021; Myrstener et al. 2021; Rashidabadi et al. 2022). Although daily mean summer water temperatures remained below 16 °C, typically within the optimal range for juvenile coho salmon (Richter and Kolmes 2005), warmer water temperatures can lead to sublethal effects such as increased energetic demand and affect behaviour and growth in food-limited conditions (Konecki et al. 1995; Railsback 2022). These findings suggest that summer food availability at these sites may not meet the metabolic demands of individual fish. Consequently, spring may be an energetically favourable period while summer may impose greater metabolic demands relative to the amount of energy available in the study system.

The shared pattern of declining energetic condition across sites suggests that temporal habitat variation, particularly during summer, exerts a strong influence on juvenile coho salmon. Given the high site fidelity of fish in the sampled streams throughout the study period (Braun, unpublished data, 2025; Scott et al. 1981), site-specific conditions likely drive the observed trends. Juvenile energetic condition typically increases with body size and fluctuates seasonally, with energy stores often peaking during transitions between favourable and unfavourable periods (Martin et al. 2017). Further research on the seasonal response in growth and energetic condition to measured changes in habitat (e.g., temperature and food availability) during critical time-periods will contribute to knowledge on how temporal habitat dynamics influence habitat quality in this system (Armstrong et al. 2021). This emphasizes the importance of considering both biotic and structural habitat aspects, as well as possible interactions between habitat variables over time in determining the effect of habitat on energetic condition.

Management implications

Linking habitat characteristics to juvenile coho salmon energetic condition can support management decisions by providing early, sensitive indicators of habitat change or quality beyond population abundance metrics. For instance, Polivka (2020) found metrics of size and energetic condition increased following habitat restoration treatments while density was unchanged. Our findings generally support this idea as energetic condition metrics varied with habitat attributes in ecologically intuitive directions. Thus, we suggest individual energetic metrics be considered for assessments of habitat quality or change, particularly over shorter time frames. Additionally, establishing baseline energetic condition thresholds required for survival could inform management targets by providing benchmarks to predict population responses and quantitatively evaluate the impacts of habitat alteration or climate-driven stressors.

The decline in energetic condition with increasing temperature, even over a moderate range, was among the strongest associations we observed. This improved understanding can provide novel insights into temperature mitigation strategies, allowing for proactive and targeted interventions for improving habitat quality. For example, our results suggest that restoration actions such as protecting and restoring riparian zones for higher shade cover to promote cooler streams (Cunningham et al. 2023; Iacarella et al. 2024) could lower metabolic costs for fish and potentially improve salmon energetic condition. Thus, maintaining optimal thermal conditions in freshwater habitats could have population-level implications through enhancing juvenile salmon growth and survival.

Individual energetic condition metrics could be used to assess habitat quality, helping inform specific management targets based on physiological thresholds. For example, using threshold metrics allows for credible predictions or even post hoc explanations of fish mortality based on habitat changes (Patterson et al. 2016). Field and laboratory studies have reported a 1.5%–2.0% lipid survival threshold for salmonids (Biro et al. 2004; Wilson et al. 2021). We observed lipid values post-winter that were in line with this reported lipid survival threshold. Specifically, most fish sampled in April had percent lipid and ED levels close to the hypothesized minimum energetic condition required for survival (2.0% lipid and 3.5–4 $\mathrm{kJ \cdot g^{-1}}$ ED). Furthermore, our results suggest that water temperatures during the growing season may impact an individual's ability to stay above this lower threshold. For example, our spatial model indicates that a 3-degree increase in the average daily stream temperature (increasing from 11 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 sized fish. Our models predict that this temperature-related lipid loss would result in decreased survival for over 29% of the population based on the fish sampled. Increased mortality rates for this proportion of the population due to temperature-related lipid loss could lead to measurable declines in population size. Our study did not directly measure overwinter survival in relation to pre-winter lipid levels; however, future studies could develop pre-winter thresholds that can be used to assess population response to warming water conditions. Taken together, this suggests that energetic condition metrics (e.g., percent lipid and ED) could be useful management indicators of the risk of warming temperatures to populations.

These findings also emphasize the importance of monitoring seasonal and habitat-driven shifts in fish energetic condition. Importantly, salmon habitats can vary substantially in quality from year to year, depending on changing temperatures and other habitat features (Brennan et al. 2019). This interannual variability highlights that ongoing monitoring of physiological responses can provide valuable guidance for management actions. Using species- and population-specific models integrating physiological data with biophysical habitat characteristics could enhance our understanding of how fish energetics respond to both temporal and spatial changes in habitat quality.

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 (Patterson et al. 2016; Iacarella and Weller 2024). The variability in juvenile coho condition metrics observed across sites and seasons highlights the influence of spatial and temporal habitat variation on energetic condition. Our findings suggest that juvenile salmon energetic condition is closely tied to specific measures of habitat (e.g., temperature, productivity) and 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 for management across species and ecosystems (Cooke et al. 2020) and using individual energetic condition as an indicator of habitat quality. Refining tools 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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Data availability

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Competing interests

The authors have no conflicts of interest to declare.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2025-0426.

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