Assessing the Consistency of Stream Ecosystem Characteristics in Accounting for Variation in Trout Abundance Between Summers with Low Versus High Flow Conditions

by
Nicole M. Miller

A THESIS

submitted to

Oregon State University

Honors College

in partial fulfillment of
the requirements for the
degree of

Honors Baccalaureate of: Science in Biology
(Honors Scholar)

Presented June 7, 2023
Commencement June 2023

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Abstract approved:____

Dana Warren

Water availability is a controlling factor in stream ecosystems with direct influences on habitat and aquatic ecosystem process, but little work has been done evaluating how biota respond to natural variations in low flow conditions during summer, and which biotic or abiotic features in the system may link most closely to aquatic vertebrates. I focus here on differences in biomass and abundance of salmonids in 16 streams in western Oregon across two years with distinctly different flow regimes that fall within the natural range of variation for summer flows in this region. Habitat is expected to be particularly important under low-flow conditions, so under higher flow conditions that provide adequate coastal cutthroat trout habitat, other factors such as food resources may be more limiting, and therefore more closely associated with local fish abundances. I found weak support for our hypotheses, but overall, the responses were not consistent across abundance or biomass density. Based on these results, I conclude that the lack of a shift towards or from any clear associations with changes in flow indicates that the system is resilient to the range of flows observed here, and/or that factors not included in my assessment are influencing trout populations.

Keywords: summer low flow, coastal cutthroat trout, abiotic characteristics, biotic characteristics, forested streams, headwater streams

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Honors Baccalaureate of Science in Biology project of Nicole M. Miller presented on June 7, 2023.

APPROVED:

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Ashley Sanders, Committee Member, representing Forest Ecosystems and Society

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Toni Doolen, Dean, Oregon State University Honors College

I understand that my project will become part of the permanent collection of Oregon State University, Honors College. My signature below authorizes release of my project to any reader upon request.

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Nicole M. Miller, Author

Introduction

Aquatic ecosystems are threatened by climate impacts that alter flow regimes. Floods and drought can disrupt the growth, survival, and population dynamics of stream fish, in addition to shifting their resource needs (Acuña et al. 2005). However, streams themselves are inherently dynamic ecosystems and the biota that live in them are therefore adapted to different flow and habitat conditions. With the goal of understanding how stream biota are likely to respond to changes associated with climate impacts, I focus here on exploring how fish populations respond to natural variation in flows and how different flow regimes may affect which components of the system are most closely associated with key population demographics.

Water availability is a controlling factor in stream ecosystems with direct influences of flow levels on habitat and ecosystem processes. Mountain streams in Mediterranean climates are well-suited to explore the effects of differences in flow as a lack of summer rain leads to natural low-flow conditions in summer (Gasith and Resh 1999, Acuña et al. 2005). Mediterranean climates are characterized by wet and relatively mild winters, and hot, dry summers, with a minimum of 65% of the precipitation in the region occurring during the winter months, but that amount often reaches over 80%, separating Mediterranean climates from other temperate regions that have less significant seasonality in their precipitation (Gasith and Resh 1999). In Mediterranean climates, summer low-flow conditions can vary greatly depending on the previous winter's precipitation and snowpack, which commonly fluctuates up to 30% away from multiannual mean amounts (Gasith and Resh 1999, Warren et al. 2015). As a result of these cyclic precipitation patterns, streams in Mediterranean climates have high variability within and among years, making them an ideal system to investigate how variation in flow regimes affects fish populations (Gasith and Resh 1999, Acuña et al. 2005).

Water availability can be a major contributor to the condition, survival, and abundance of stream biota, especially vertebrates such as salmonids in headwater ecosystems. Stream discharge dictates the functional habitat available for these species, particularly in small streams, where habitat is already limited. Droughts have especially severe effects on salmonids in small streams by greatly reducing habitat availability, as well as overall water quality, since low flows are often associated with reduced DO levels and changes in physiochemical conditions that can affect fish survival (Acuña et al. 2005, Warren et al. 2015, Deitch et al. 2018). Earlier drought studies in headwaters have shown that greater pool depths, and connectivity between pools in particular are associated with improved survival and greater abundance of trout in headwater streams during periods of drought (Kaylor et al. 2019, Sheldon 2010). Manipulative and correlative field studies have also demonstrated the critical role of habitat availability in headwater streams (Roni et al. 2008, White et al. 2011), and in a study in more controlled experimental channels, Halbert and Keeley (2023) found a clear positive correlation between pool habitat area and *Oncorhynchus clarkii* density.

In addition to habitat, salmonids are also influenced by food resources. Generally, increasing food availability in streams increases growth rates and survival of salmonids, with clear implications for overall salmonid populations. Food availability and habitat can be limiting factors for fish production in headwater streams individually, but these factors can also interact and the factor(s) that limit production and growth of fish in a stream can change over time (Rose and Oliver 2017). If there is adequate pool availability, habitat would be less likely to limit fish and the population would be limited by some other factor – such as food (Wilzbach 2011). Conversely, if food is adequate, populations are more likely to be limited by habitat (Chapman 1966). With changes in flow come changes in habitat, therefore, a change in flow could shift the relative importance of habitat versus food availability when it comes to predicting trout abundance and growth, particularly in small headwater streams where deep pools may be scarce (Hakala and Hartman 2004). In circumstances where there is an adequate amount of functional habitat available for fish (i.e.: average to high-flow years), factors related to basal resource availability should grow relatively more important in predicting trout condition and abundance, rather than factors relating to habitat, since those requirements will be met by the level of flow. During periods of low-flow and drought, food and basal resource availability is expected to be less important than factors related to habitat, particularly components directly related to water availability such as pool depth, area, and connectivity(Penaluna et al. 2021). I hypothesized therefore that in 2022, a relatively high flow year in western Oregon (65th percentile in mean daily discharge rate out of historical data), metrics related to food availability will be the most significant explanatory variables predicting the abundance of cutthroat trout*,* because habitat is not as limited by flow, while in 2021, the relatively low flow year (65th percentile in mean daily discharge rate out of historical data), metrics related to water, and therefore, functional habitat availability will be the most significant explanatory variables predicting the abundance of cutthroat trout*,* because lower flows will restrict the area of available habitat.

Due to their differing habitat requirements and ability to access different areas in streams (e.g., channel margins and hyporheic habitat), fish of different size and age classes may be affected differently by changes in flow. In addition, young-of-year (YOY) tend to consume smaller macroinvertebrates, while adult trout eat a larger range of macroinvertebrates as well as other vertebrates, which opens the potential for a differential effect of flow on adults vs. YOY fish (Kelly-Quinn and Bracken 1990). The physical conditions that are optimal for salmonids also differ between young-of-year and adult fish, which means that a differential effect of flow on trout of different age classes could also arise from changes in the availability of different types of habitat within streams (Chapman 1966, Rosenfeld et al. 2007).

Understanding how the current natural variation in low flow affects the relative importance of different stream characteristics for salmonids in headwater streams is important for informing future forestry and fishery management strategies, as the effects of climate change are expected to further exacerbate variability in environmental conditions that affect stream regimes, such as precipitation rates and snowpack levels, temperature increases, wildfire frequency and intensity, and changes in the frequency and intensity of other disturbances (Filipe et al. 2013). In this study, I evaluate how populations of *Oncorhynchus clarkii clarkii* (Coastal Cutthroat Trout) relate to stream habitat characteristics and basal resource availability over two years that encompass summer flows at the upper and lower ranges of natural variation (within the 24th and 65th percentiles of the annual summer low flow) in a Mediterranean ecosystem. Specifically, this study investigates whether abiotic factors (pertaining to habitat availability and quality) or biotic factors (pertaining to basal resource availability) are more limiting when it comes to the abundance of *Oncorhynchus clarkii clarkii* in headwater streams, and if there is a difference in the most important factors between adults and young-of-year.

Methods

Study sites

This study evaluated sixteen 1st and 2nd order streams in the Oregon Coast Range between the latitudes 43.97325 and 46.0397 (Table 1). All streams were small, with mean bankfull widths under 5 m, and all sites had intact second-growth riparian forests dominated by Red Alder (*Alnus ruba*), Western Cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*). The years in which the streams were sampled differed greatly in flow conditions. Data from long-term records at the Siletz River – a system the western Coast Range that has had continuous flow gaging since 1983—show that 2021 was a relatively dry year while 2022 was a relatively wet year (Figure 2). Flows during the summer in these years encompass a wide range of variation in flows while keeping without extending to extreme drought or extreme high flow conditions. In 2021, daily flows were at the 24th percentile of all available data, and in 2022, they were at the 65th percentile.

Figure 1: Map of study sites

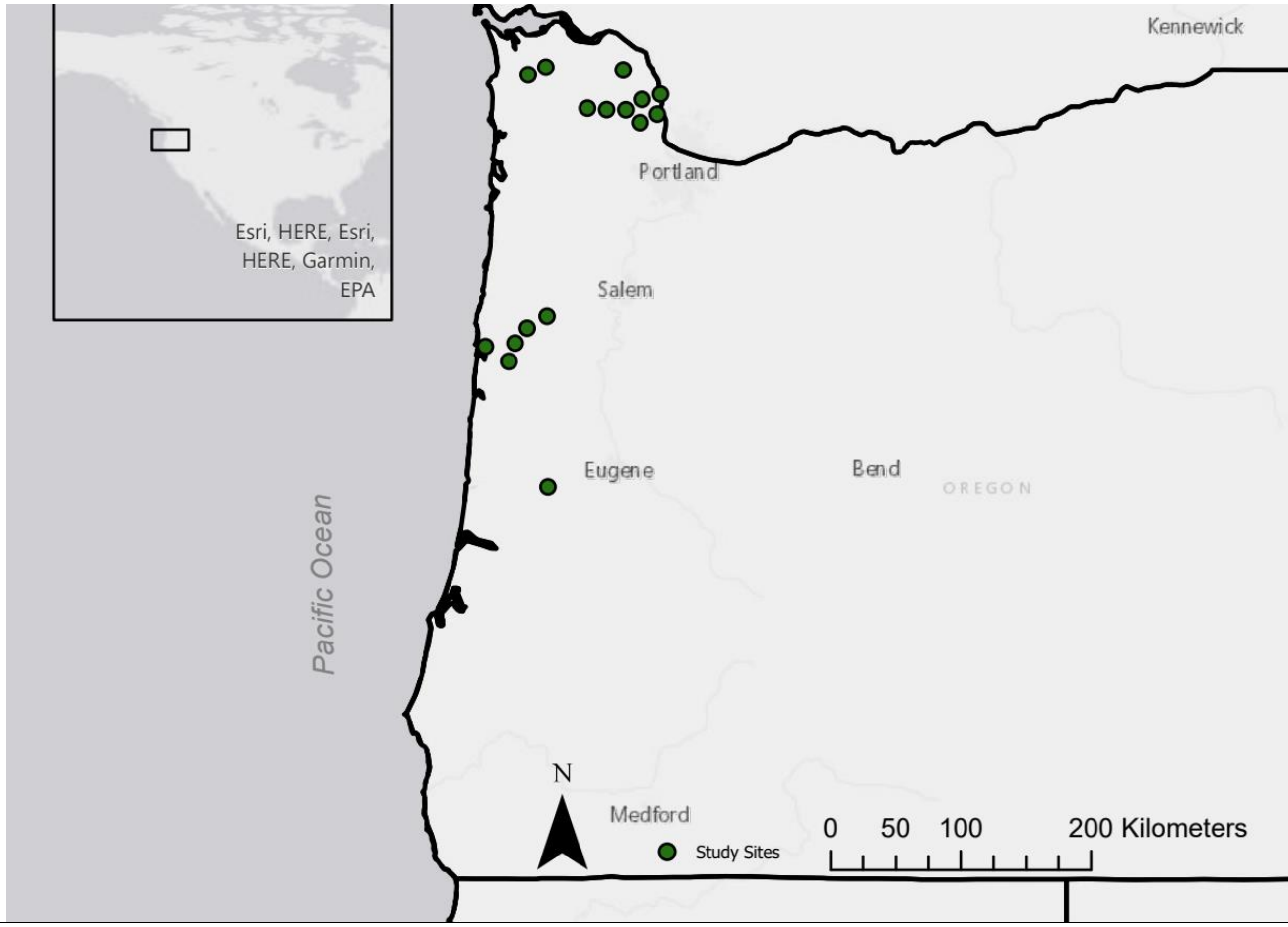


Fig 1: *Map of sites used in this study, marked in green points*

Table 1: Characteristics of the sixteen streams used in this study

Site	Block	Coordinates	Elevation (m)	Total Reach Length (m)	Fishing Reach Length (m)	Mean Bankfull Width (m)
CH	Astoria	46.01715, -123.5892	351.66	200	68	3.26
SL	Astoria	45.9937, -123.6689	217.97	200	80	4.18
TG	Newport	44.66429, -124.0062	51.88	200	65	2.17
SA	Newport	44.74554, -123.7281	129.95	200	60	1.75
WS	Newport	44.61948, -123.8309	109.14	200	60	1.63
GD	Newport	44.68094, -123.8014	97.85	200	60	1.29
CS	Scappoose	45.8143, -123.0926	329.56	200	62	4.51
GB	Scappoose	45.81406, -123.0762	425.44	200	60	4.51
LA	Scappoose	45.80369, -123.0193	289.52	200	60	2.51
OJ	Scappoose	45.79184, -122.9698	291.25	200	60	3.14
ST	Scappoose	45.80736, -123.0281	273.33	200	60	4.32
GF	Vernonia	45.81325, -123.0374	295.21	200	60	2.13
MS	Vernonia	45.81412, -123.038	299.85	200	60	2.51
BR	Vernonia	46.00397, -123.0556	244.91	200	60	3.75
HB	Valsetz	44.80389, -123.629	264.74	300	90	1.86
SR	Walton	43.97325, -123.5746	153.51	300	90	2.80

Figure 2: Historical flow records at Siletz River (USGS gage #14305500)

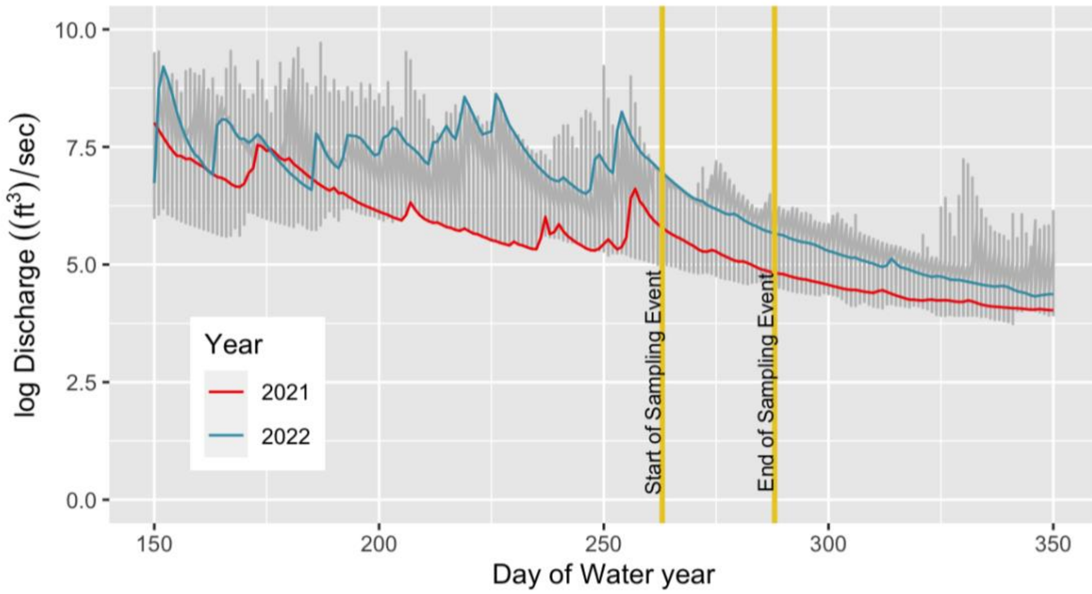


Figure 2. *Long-term flow records at the Siletz River gages (gage #) relative to the two focal years for this study. All historical data are plotted in grey, and the study years are plotted in red and blue. Vertical yellow lines indicate the approximate start and end dates for fish sampling across the 16 study streams in both years.*

Study Design

This study surveys trout abundances across 16 different headwater streams over two years, that represented relatively high and relatively low-flow conditions within that natural range of summer flow variation that occurs in this region. I collected data on the abundance of adult (1+ and older) and young-of-year (age 0+) trout as the key response metrics for this study. I also collected data on a suite of biotic and abiotic features in the system which I used to evaluate the hypothesis that different metrics of habitat versus food resources (or proxies thereof) would have different degrees of relative importance in explaining variation in fish abundances and total biomass across the study streams in years with lower or higher summer low flow conditions. I expected biotic metrics to better explain variation in fish abundance in high flow years (as I expected some release from habitat limitation), and I expected abiotic metrics to better explain variation in fish abundance in low-flow years (as reduced water would limit habitat availability in the system). I evaluated these expectation using a series of linear models which were compared qualitatively with a correlation matrix and then quantitatively with multiple linear regression followed by Hurvich and Tsai's corrected Aikikes Information Criteria (AICc) analysis (1989).

Data Collection

Fish

Adult and young-of-year (YOY) *Oncorhynchus clarkii clarkii* populations were sampled from a subset of each stream reach (referred to as the "fishing reach") via a three-pass depletion method using backpack electrofishing (Smith-Root Model LR-20B). Each end of the fishing reach was secured using block nets to ensure a closed population was sampled, and fishing effort remained consistent across all three passes. Upon capture, fish were measured (total length and fork length—both in mm) and weighed, then returned to the same area of the stream from which they were removed from. Adult and young-of-year *Oncorhynchus clarkii clarkii* populations were estimated separately using the Lincoln-Peterson method.

Abiotic metrics

Stream geomorphology surveys were conducted to quantify parameters including bankfull width, wetted width, stream depth, and pool area and depth. The bankfull width, wetted width, and stream depth were measured at eight evenly spaced transects in each stream along the larger reach. The surface area, maximum depth, and outflow depth of all pools within the fishing reach were measured and used to calculate the mean maximum pool depths and total pool area. Canopy cover was measured using a densiometer at eight evenly spaced locations along each stream. Temperature data was collected using HOBO TidbiT v2 temperature logger (accuracy ±0.27C; Onset, Bourne, Massachusetts, USA). which recorded temperature every hour. We had overlap across all sites and years for the months of June-August so data from these months were used to compare summer temperature dynamics.

Biotic metrics

Periphyton was collected from natural substrates to measure ash-free dry mass (AFDM) at five sampling locations evenly-spaced within each stream's complete reach. Each sampling location produces one sample, resulting in 5 samples per stream, from which the mean AFDM was calculated. Benthic macroinvertebrates were collected using a Surber sampler with 0.093m^2 area and 247¬µm mesh. Surber samples were collected at five riffle locations evenly spaced through the larger study reach, from which the five samples per stream were compiled into a single pooled sample for each stream. The pools samples were stored in ethanol and then sent to Benthic Aquatic Research Services for identification (to genus or species, except *Chironomids*, which were identified to just the family) and enumeration. Because *Ephemeroptera*, *Plecoptera*, and *Tricoptera* orders are often key food resources for fish and because their abundances can vary with stream productivity and condition, we focused on the total abundance of these "EPT" taxa as a metric to represent potential in-stream food availability (EPT index).

Data Analysis

To assess the degree to which abiotic and biotic factors explained the abundance and biomass density of adult and young-of-year *O. clarkii clarkii*, we conducted multiple linear regression analysis and used the corrected Aikikes Information Criteria (AICc) analysis to select the parameters of the linear regression model that best fit the data (Hurvich and Tsai 1989). The abiotic variables used were total pool area, which is the sum of the surface areas of all pools within a site's fishing reach, mean maximum pool depth, which is the mean of the maximum depth of all pools within each stream's fishing reach, temperature, which was calculated from the mean daily temperatures in August each year, and mean canopy cover. The biotic factors were the EPT richness index and mean periphyton ash-free dry mass (ADFM). The response variables were density of adult Cutthroat Trout (per m), biomass density (per meter) of adult Cutthroat Trout, density of young-of-year Cutthroat Trout (per m), and biomass density (per meter) of young-of-year Cutthroat Trout. The data for the canopy cover, EPT index, and adult cutthroat biomass density were all log transformed to improve normality before statistical analysis was conducted.

Results

In 2021 we collected a total of 244 age 1+ and older cutthroat and 587 young-of-year cutthroat. In evaluating factors associated with adult cutthroat biomass density, the correlation analysis indicated that periphyton ash-free dry mass was most closely associated, however in contrast to our expectations, the relationship was negative (r =-0.286). Total pool area and mean summer temperature were also somewhat correlated (r = 0.283, and r = 0.245 for pool area and summer temperature respectively (Figure 2A; Appendix 2A). In the 2021 AIC analysis, the best model to account for variation in adult trout biomass density during this low-flow year was the null model, with ash-free dry mass and total pool area alone as models that also had delta AIC <2 (Table 7A, Appendix 3A). Adult trout density (number per meter squared) in summer 2021 had similar results to biomass density overall. Adult trout density was also most strongly correlated with periphyton ash-free dry mass (-0.29), however the other top correlates for this metric were canopy cover and mean maximum pool depth (Table 5A, Appendix 2A). In the AIC model comparison for adult trout density, the best model in 2021 was also the null model among the parameterized models, ash-free dry mass as the only other model with a delta AIC< 2 (Table 5A, Appendix 2A).

The cumulative AIC weights for each metric in 2021 for models linked to adult trout biomass indicated that benthic biofilm AFDM was the best collective metric. AFDM had the largest cumulative weight, followed by mean of maximum daily summer temperature (Table 4). Results for adult trout density were somewhat comparable: AFDM was also the top metric in models accounting for adult trout density in 2021, but the second-best metric in summed AIC weights was canopy cover and then density of EPT (Table 3).

For young-of-year trout in 2021, the correlation matrix assessing factors associated with young-of-year density (number per m) indicated that in this dry year, maximum pool depth was most strongly (and positively) related to young-of-year density (0.32), followed by EPT and mean of maximum daily summer temperature (Table 3A, appendix 2). As with adult trout, the AIC analysis also selected the null model as the best model to account for young-of-year density. Among the models that included stream characteristic parameters, the best model included mean of maximum pool depth alone, followed by a model that included the density of EPT macroinvertebrate taxa alone (Table 2) the AIC analysis of young-of-year trout biomass (per meter squared) also had mean of maximum pool depth as the best of the parameterized model. In the assessment of cumulative AIC weights, mean of maximum pool depth was the top metric, followed by the abundance of EPT taxa for the models of young-of-year population density and young-of-year biomass density (Tables 5 and 6).

In 2022, we captured a total of 186 age 1+ and older adult cutthroat and 433 young-of-year CT. In evaluating factors associated with adult cutthroat biomass density in this wet year, the correlation analysis indicated total pool area was most closely correlated, although the relationship was negative (-0.30 ; Figure 4), followed by periphyton ash-free dry mass (Table 2A; Appendix 2A). In the 2022 AIC analysis, the best model for the biomass density of adult trout was again, the null model. Total pool area and periphyton ash-free dry mass + mean summer temperature were the next best models, both of which had delta AIC value <2 (Table 8A, Appendix 3A). For adult trout density, the best model in 2022 was also the null model. Adult cutthroat density was found to be most strongly correlated with mean summer temperature (0.17), mean maximum pool depth, and total pool area (Table 2A, Appendix 2A). The best of the models that included stream metrics were mean of maximum pool depth and mean of daily maximum stream temperature. However, one of these other models for trout density in 2022 had delta AIC values less than 2 (Table 8A, Appendix 3A). The assessment of cumulative AIC wights for each metric for the adult cutthroat density in 2022 indicated that summer temperature was the best metric followed by biofilm AFDM. For biomass density of adult fish, the summed weights were equal for both temperature and biofilm AFDM (Table 4).

Total pool area and the abundance of EPT taxa were the metrics most strongly correlated with young-of-year density in the wetter summer of 2022 (r= 0.24 and 0.16 for pool area and EPT, respectively), followed by EPT and mean periphyton ash-free dry mass (Figures 5, 6, and Table 3A, Appendix 2A). In the AIC analysis of YOY abundance in 2022, the null model was selected as the best linear model and was the only model with an AIC value less than 2 (Table 10, Appendix 3A). The assessment of cumulative AIC weights for the models of young-of-year density showed that EPT and total pool area were tied for the highest net weight (0.17), followed by mean summer temperature for both YOY population densities and YOY biomass densities (Table 5). Adult cutthroat densities and biomass densities had similar ranges across years (0 to 0.4 fish/m, but modes shifted among years (Figures 7, 8). YOY cutthroat abundance and biomass densities had similar modes across years, but the overall range of densities was greater in 2021 (Figure 9, 10).

Figures and Tables

Figure 3: Correlations between adult trout density and stream characteristics

a: Lower-flow year   b: Higher-flow year

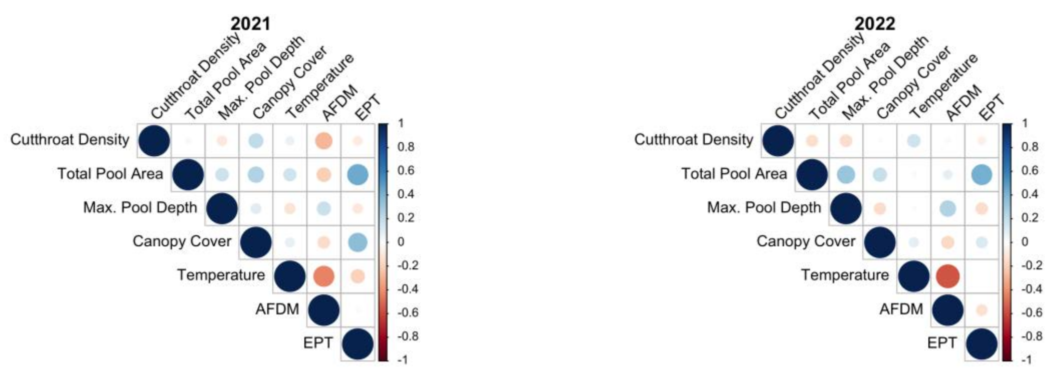
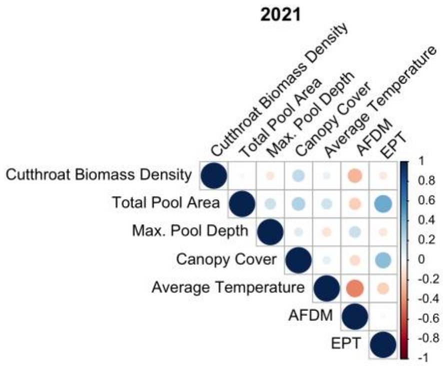


Fig 3: Correlations between Adult cutthroat density and stream characteristics, and among stream characteristics in 2021 and 2022.

Figure 4: Correlations between adult trout biomass density and stream characteristics

a: Lower- flow year



b: Higher- flow year

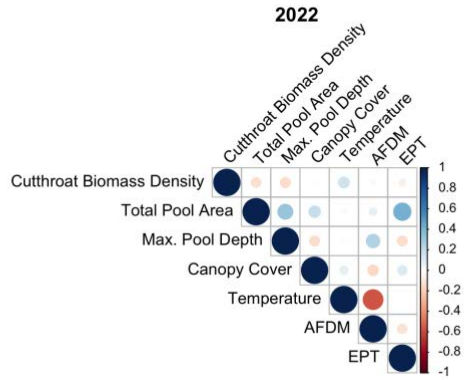
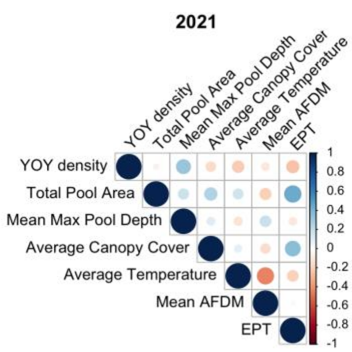


Fig. 4: Correlations between Adult cutthroat biomass density and stream characteristics, and among stream characteristics in 2021 and 2022.

Figure 5: Correlations between young-of-year density and stream characteristics

a: Lower- flow year



b: Higher- flow year

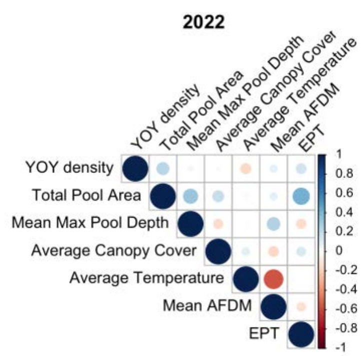
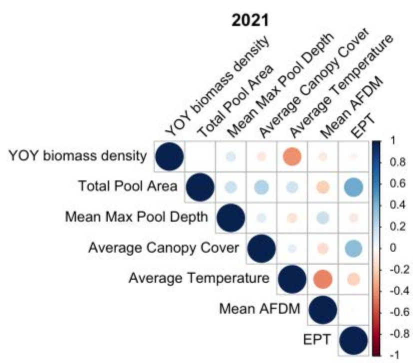


Fig. 5: Correlations between YOY density and stream characteristics, and among stream characteristics in 2021 and 2022.

Figure 6: Correlations between young-of-year biomass density and stream characteristics

a: Lower-flow year



b: Higher- flow year

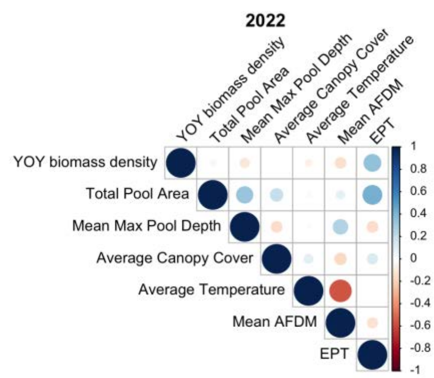


Fig. 6: Correlations between YOY biomass density and stream characteristics, and among stream characteristics in 2021 and 2022

Table 2: Top AICc models for each response variable

	Year	Model	Delta AIC
Adult cutthroat Density	2021	Null	0
		AFDM	1.71
	2022	Null	0
Adult cutthroat Biomass Density	2021	Null	0
		AFDM	1.71
		PLA	1.74
	2022	Null	0
		PLA	1.57
		AFDM +TMP	1.61
Young-of-year Density	2021	Null	0
		MMD	1.31
	2022	Null	0
Young-of-year Biomass Density	2021	Null	0
		MMD	1.31
	2022	Null	0

***Table 2:** AICc models with a delta AICc <2.00 for each response variable and year.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, EPT = EPT index, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 3: Summed AIC weight of model parameters for adult cutthroat density

a: Lower-flow year (2021)			**b:** Higher-flow year (2022)	
Metric	Cumulative AIC weight		Metric	Cumulative AIC weight
AFDM	0.21		TMP	0.17
CAN	0.18		AFDM	0.14
EPT	0.12		PLA	0.13
TMP	0.12		EPT	0.13
PLA	0.11		CAN	0.12
MMD	0.11		MMD	0.12

Table 3: *Summed AIC weight across all models for adult CT density (per m) including each of the stream characteristics metrics in the AIC analysis for adult trout in 2021 and 2022.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, EPT = EPT index, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 4: Summed AIC weight of model parameters for adult cutthroat biomass density

a: Lower-flow year (2021)			**b:** Higher-flow year (2022)	
Metric	Cumulative AIC weight		Metric	Cumulative AIC weight
AFDM	0.20		AFDM	0.26
TMP	0.19		TMP	0.26
EPT	0.15		PLA	0.19
CAN	0.15		EPT	0.13
PLA	0.10		CAN	0.13
MMD	0. 09		MMD	0.08

Table 4: *Summed AIC weight across all models for adult CT biomass density (per m) including each of the stream characteristics metrics in the AIC analysis for adult trout in 2021 and 2022.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, EPT = EPT index, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 5: Summed AIC weight of model parameters for young-of-year density

a: Lower-flow year (2021)		**b:** Higher-flow year (2022)	
Metric	Cumulative AIC weight	Metric	Cumulative AIC weight
MMD	0.20	EPT	0.17
EPT	0.19	PLA	0.17
TMP	0.17	TMP	0.15
AFDM	0.15	AFDM	0.14
CAN	0.13	CAN	0.13
PLA	0.10	MMD	0.09

Table 5: *Summed AIC weight across all models for YOY density including each of the stream characteristics metrics in the AIC analysis for adult trout in 2021 and 2022.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, EPT = EPT index, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 6: Summed AIC weight of model parameters for young-of-year biomass density

a: Lower-flow year (2021)		**b:** Lower-flow year (2022)	
Metric	Cumulative AIC weight	Metric	Cumulative AIC weight
MMD	0.20	Total pool area	0.17
EPT	0.19	EPT	0.17
Average Temp	0.15	Average Temp	0.15
Can	0.15	Can	0.13
AFDM	0.15	AFDM	0.12
PLA	0.10	MMD	0.09

Table 6: Summed AIC weight across all models for YOY biomass density including each of the stream characteristics metrics in the AIC analysis for adult trout in 2021 and 2022.
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, EPT = EPT index, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Figure 7: Histogram of adult cutthroat density

a: Lower-flow year (2021) **b:** Lower-flow year (2022)

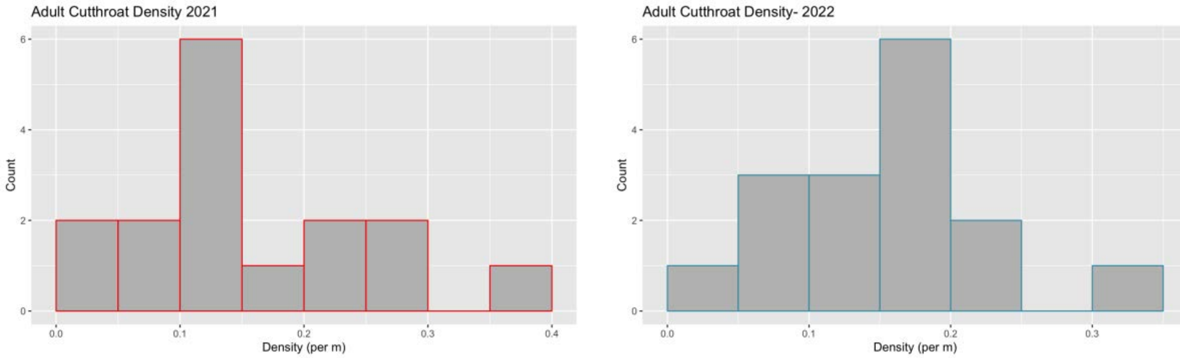


Fig. 7: Histograms depicting the distribution of densities for adult Cutthroat Trout in 2021 and 2022.

Figure 8: Histogram of adult cutthroat biomass density

a: Lower-flow year (2021) **b:** Higher -flow year (2022)

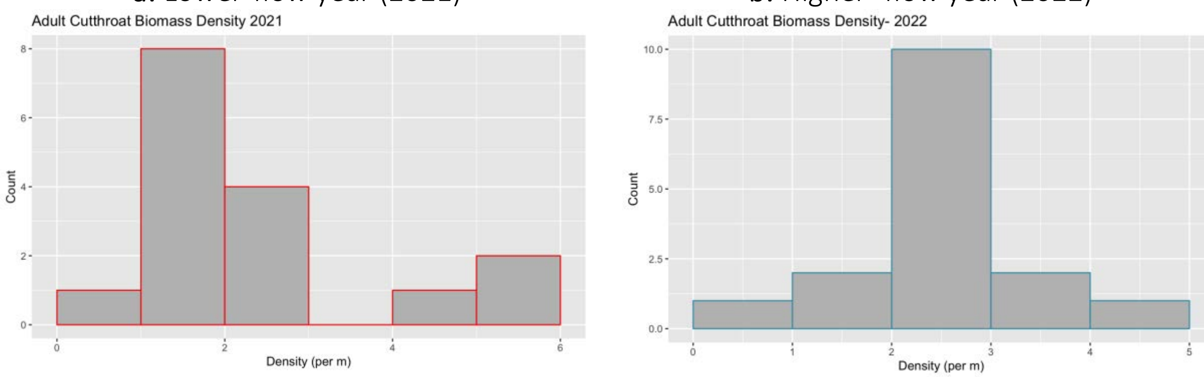


Fig 8: *Histograms depicting the distribution of biomass densities (in g/m)for adult Cutthroat Trout in 2021 and 2022. These data were log-transformed to achieve normality.*

Figure 9: Histogram of young-of-year cutthroat density

a: Lower-flow year (2021) **b:** Higher-flow year (2022)

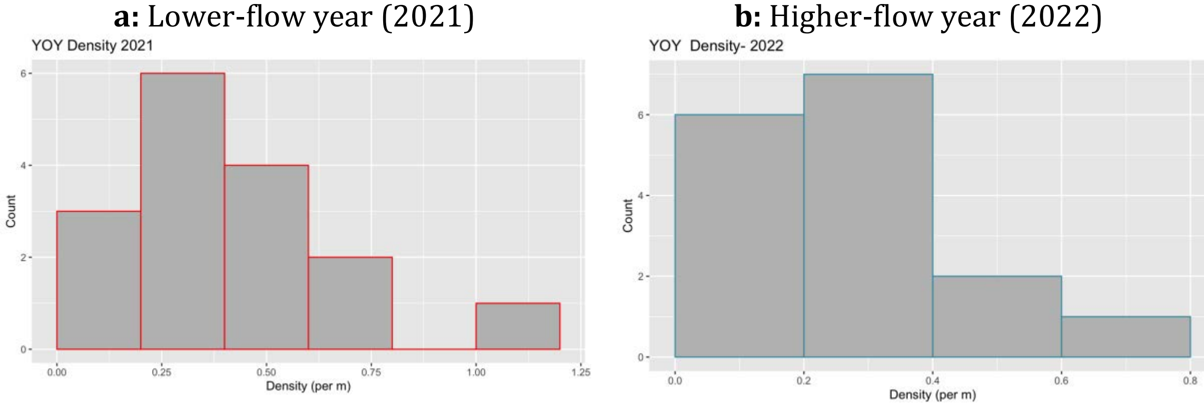


Fig 9: *Histograms depicting the distribution of densities for young-of-year trout in 2021 and 2022.*

Figure 10: Histogram of young-of-year biomass density

a: Lower-flow year (2021) b: Higher -flow year (2022)

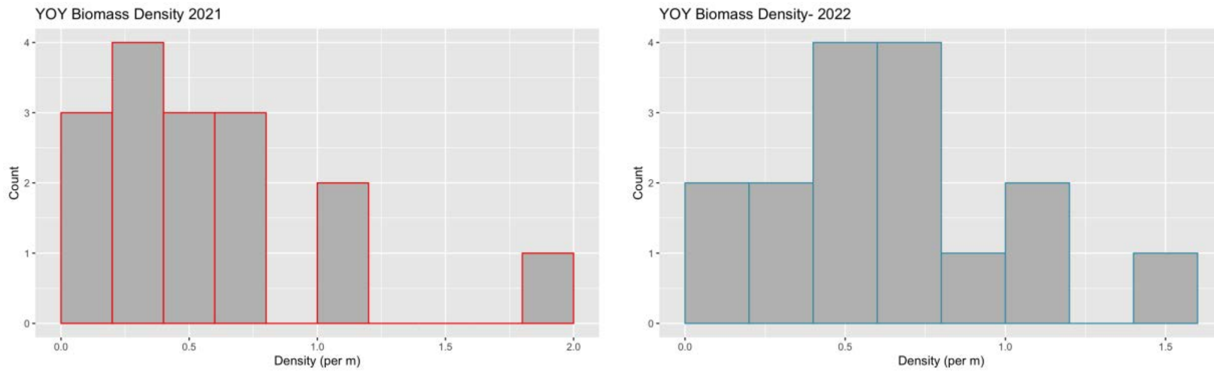


Fig. 10: Histograms depicting the distribution of biomass densities (in g/m) for young-of-year *trout in 2021 and 2022.*

Discussion

Many studies look at the effects of floods and droughts on fish communities, but there is natural variation in flow conditions that are often overlooked. This study explored factors linked to abundance and biomass of adult and juvenile trout in headwater streams during years that encompass the upper and lower ranges of natural summer flow variation. We expected abiotic metrics associated with pool habitat to be best correlated with trout populations in the low-flow year in our study (2021), and we expected biotic metrics associated with food availability to be the best correlate with trout in a high flow year – reflecting hypothesized shifts in limiting resources for trout with changing flow regimes. Across our sixteen study streams, we found limited support for these hypotheses. The correlation analysis indicated surprisingly few strong relationships between trout and any of our independent variables, and across the board, the AIC analysis indicated that the null model outperformed our metrics individually or in combination. The sum of AIC weights for all models containing each metric did not provide support for our hypotheses for adult trout biomass, but the summed AIC weight result did provide slight support for our hypotheses regarding YOY trout. There were changes in the relative importance of maximum pool depth models between 2021 and 2022 that were consistent with our expectations. Mean of maximum daily pool depth was the top metric in 2021 when flows were low, but the worst metric in 2022 when flow was elevated. However, there was not a comparable shift in the rank of food resource metrics in YOY trout models between summer 2021 and 2022, which would have provided stronger support for our overall hypotheses.

Adult trout

Regarding the density of adult cutthroat, periphyton ash-free dry mass was one of the most important variables in the lower-flow year, with the 2021 analyses indicating it had the strongest correlation with CT density and the highest cumulative AIC weight and was selected as the second-best AIC model. However, in contrast to our expectations, the correlation between periphyton AFDM and trout abundance was negative in the low-flow summer (2021). In summer 2022 when flows were above average, periphyton AFDM was no longer negatively correlated with trout densities, but no other metric arose as a key correlate for trout density in this year and AFDM was still one of the top two metrics for adult trout population density and biomass density.

Surprisingly, our results suggested that none of the metrics we identified as likely being linked to fish abundance were strong predictors but were in fact poor predictors – both alone and in combination with other metrics of adult trout populations. All correlation values in summer 2022 for trout density were $<|0.15|$, and over both years, the null model in the AIC analysis was more parsimonious than any of the models that included one or more metrics. This was unexpected, since we explicitly sought to encompass well-established habitat metrics and both direct and indirect food resource metrics that have been linked to fish abundance in other systems (Hayes et al. 2007, Rosenfeld and Taylor 2009, Kaylor et al. 2019).

Results for adult trout biomass were consistent with those of trout abundance regarding the negative relationship with periphyton AFDM in summer 2021 and in the overall lack of correlations with adult trout in summer 2021 or 2022. Similarly, the null model also outperformed the models with our selected metrics for adult trout biomass in summer 2022. This summed AIC weight metric is recommended by Burnham and Andersen (2004), as an integrated metric that can account for variation across model sets when comparing the relative importance of individual metrics. Because this metric can be affected by the number of models that each metric appears in, we made a point of creating a balanced total model set. however, mean of maximum pool depth was included in only 4 models while the rest were included in 5. This likely had little influence on the overall results though since the mean of maximum pool depth was generally either a top model anyway, or so low in the ranking that small changes associated with being included in another model would make no difference. In the summed analysis, the individual metric with the most overall "importance" for trout density in 2021 was AFDM, which is contrary to our prediction for low-flow conditions. We predicted that biotic factors related to food abundance would be less important during low-flow conditions based on the prediction that habitat is a more limiting factor of trout abundance, but this suggests that food availability may be of higher importance relative than we previously thought. In the higher-flow year, abiotic factors were more closely linked to adult cutthroat density, which is contradictory to my hypothesis that biotic (specifically food-related) factors would be most closely linked to adult cutthroat density. Mean summer temperature had the highest net AIC weight and correlation values and was the second-best model according to the AIC selection.

Young-of-Year (YOY) Trout

Our prediction that YOY abundance and biomass density would be linked to metrics associated with functional habitat during the lower-flow year was weakly supported. Maximum pool depth was the metric most closely related with both YOY abundance and biomass density in 2021. This follows previous findings detailing the importance of pool habitats for YOY growth (Rosenfeld and Taylor 2009). However, these correlation values were still weak, and the null model was selected as the top model during the AIC analysis for both YOY abundance and biomass density, so our hypothesis was not supported to the degree that was expected. In a similar matter, our hypothesis that during the higher-flow year, YOY abundance and biomass density would be best associated with biotic variables associated with food availability was slightly supported when it came to YOY biomass density, which had the strongest correlation with EPT in 2022. EPT abundance was among the top 2 metrics for summer 2022, however it was also the second-best metric in summer 2021, and the other top metric in 2022, was pool area.

Overall, our analyses did not identify any strong patterns in the relative importance of our selected stream characteristics in predicting the abundance and biomass density of both adult and YOY cutthroat trout. Our initial question focused on whether the factors that influence fish populations in streams changes between stream flows representing high flow and low flow conditions within the region's natural range of variation (in this case, between the 24th and 65th percentiles). We expected pool habitats to be more important factors accounting for variation in the low flow year because pool depth has been identified as an essential feature in drought years, in addition to being generally known to be important habitat for fish—adults in particular (Kaylor et al. 2019). However, work by Elliott (2000) found that when selecting pools as refugia during drought years, trout preferentially selected pools within specific ranges of water temperature and dissolved oxygen levels, so those metrics may be necessary components of a multiple linear regression model that predicts trout abundance using a metric representing pool area (such as pool depth or surface area) as one of its explanatory variables. This is one possible explanation for why MMD or PLA alone were never ranked higher than the null model in any of the AIC analyses, because the interaction between pool size and water quality may be what affects fish densities within pools.

It is also possible that the difference between flows in our study years was not extreme enough for there to be an observable difference in what characteristics affect trout presence and density. Considering that Mediterranean-type streams vary greatly in annual low flow rates, it is reasonable to expect that stream biota are well-enough adapted to survive fluctuating conditions that in order for the stream characteristics we investigated to significantly alter their abundance, flows would have to be outside of their natural range in variability (Acuña et al. 2005).

This relates to our predictions for the high-flow year as well, in which we predicted that food resources (or proxies thereof) would be the most important predictors of trout biomass and density, because presumably, habitat would be less limiting. We saw weak support for these hypotheses in a few cases, but the responses were not consistent between biomass and abundance metrics or between adult and juvenile trout. The absence of a consistent shift in the factors that best account for variations in fish populations corroborates the hypothesis that the range of flows observed between these two years were not large enough did to substantially alter the core drivers of fish abundance in these systems. This suggests that although these flow changes appeared dramatically different, this natural range of flows encompassed by this study did not lead to a shift in functionality in the system.

Our initial hypotheses regarding the importance of food versus habitat with changes in flow levels between years missed the key role of streamflow in delivering food to fish via drift, which is a major influence on food availability as it carries food sources produced in riffles or on land are to other parts of the stream. This food delivery is influenced by water velocity and so] inherently links flow and food availability (Hayes et al. 2007). Trout commonly feed from the drift, in addition to the benthos, the water column, and the surface of the stream (Chapman 1966, Johansen et al. 2005, Erős et al. 2012). The availability of food in the drift is a product of both underlying invertebrate production (source populations), and stream velocities, which entrain invertebrates and deliver them to waiting fish (Hayes et al. 2007). While a reduction in stream flow may concentrate the invertebrate community into a smaller area of stream, thereby potentially increasing their vulnerability to predation by trout, reduced flows also lead to fewer invertebrates in the drift and a slower rate of delivery. Manipulative experiments have found that trout density is positively correlated with the density of macroinvertebrates in the drift, so a decrease in drift density would be expected to contribute to a decrease in trout density, by association (Slaney and Northcote 1974)

Another biotic factor that pertains to food abundance but was not included in our analyses is competition. First- and second-order streams in the Oregon coast range where *Oncorhynchus clarkii clarkii* are found also frequently contain *Oncorhynchus kisutch* (coho salmon), Cottus perplexus (Reticulate Sculpin), and *Dicamptodon tenebrosus* (Coastal Giant Salamanders), all of whose fundamental niches have some degree of overlap with that of the coastal cutthroat trout, and therefore, all compete with trout in some form (Sabo and Pauley

1997, Falke et al. 2020).   Trout in streams often compete for access to optimal foraging sites that provide high rates of invertebrate delivery in the drift while requiring minimal energetic costs, as these sites allow for more efficient foraging (Fausch and White 1981). This ties competition to flow, as the rate of invertebrate drift is directly affected by discharge, further illustrating the complex interactions between abiotic and biotic processes that characterize streams (Hayes et al. 2007).

As hypothesized by Chapman (1966), the link between food availability and flow probably means that both factors are important in predicting the abundance of trout in streams, and one does not have an exceedingly greater importance than the other during normal conditions. If this hypothesis is true, it would explain why the null model was selected as the top model during each of the AIC analyses, because there was not a big enough difference in the relative influence of different metrics on trout abundance both within and between years. It is possible that there are scenarios in which a shift of the relative importance of these factors will occur, resulting in one (or more) of these metrics acting as a dominant limiting factor on trout, however, the environmental conditions encompassed in this study were not extreme enough for this shift to occur. Based on the weak support from all of our independent variables, we can infer that other factors that we did not assess are influencing trout populations (such as DO concentration, or competition, as discussed above), but we can also draw the conclusion that the fact that the systems did not shift toward or from clear associations with these changes in flow indicated that the system is resilient to the range of flows observed here.

Conclusion

This study examined the strength of biotic and abiotic stream characteristics for predicting the abundance and biomass density of adult and young-of-year coastal cutthroat trout in headwater streams between years with relatively high and low flows that fell within the range of natural variation. We hypothesized that in the lower-flow year, variables that directly represent functional habitat availability such as maximum pool depth and total pool area would be most important, while in the higher-flow year, variables pertaining to food abundance such as periphyton ash-free dry mass and the EPT index would be the most relevant. We found weak support for these hypotheses in a few analyses, but overall, the responses were not consistent across abundance and biomass density for adult or young-of-year trout. In AIC analyses, no metric outperformed the null model for any of the response variables in either year.

A possible explanation of these results is that variables that were not included in the study—such as water quality or interspecific competition—may interact with some of the metrics we investigated and are therefore required to be included in a multiple linear regression with said metrics to create a model predicting trout abundance and/or biomass density. Alternatively, the absence of a consistent shift in the factors that best account for variations in fish populations suggests that the range of flows observed between these two years were not large enough did to substantially alter the core drivers of fish abundance in these systems. This suggests that although these flow changes appeared dramatically different, this natural range of flows encompassed by this study did not lead to a shift functionality in the system. Further research may focus on other characteristics used to model the abundance of trout, how the same metrics affect trout across years with a more pronounced difference in flow.

References

Acuña, V., I. Muñoz, A. Giorgi, M. Omella, F. Sabater, and S. Sabater. 2005. Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. Journal of the North American Benthological Society 24:919–933.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33:261–304.

Chapman, D. W. 1966. Food and Space as Regulators of Salmonid Populations in Streams. The American Naturalist 100:345–357.

Deitch, M. J., M. Van Docto, M. Obedzinski, S. P. Nossaman, and A. Bartshire. 2018, June 28. Impact of multi-annual drought on streamflow and habitat in coastal California salmonid streams. https://www.tandfonline.com/doi/epdf/10.1080/02626667.2018.1492722?needAccess=true&role=button.

Elliott, J. M. 2000. Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. Journal of Fish Biology 56:938–948.

Erős, T., P. Gustafsson, L. A. Greenberg, and E. Bergman. 2012. Forest-Stream Linkages: Effects of Terrestrial Invertebrate Input and Light on Diet and Growth of Brown Trout (Salmo trutta) in a Boreal Forest Stream. PLOS ONE 7:e36462.

Falke, L. P., J. S. Henderson, M. Novak, and D. L. Preston. 2020. Temporal shifts in intraspecific and interspecific diet variation among 3 stream predators. Freshwater Science 39:115–125.

Fausch, K. D., and R. J. White. 1981. Competition Between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for Positions in a Michigan Stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Filipe, A. F., J. E. Lawrence, and N. Bonada. 2013. Vulnerability of stream biota to climate change in mediterraneanclimates: a synthesis of ecological responses and conservation challenges. Hydrobiologia:331–351.

Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean Climate Regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events. Annual Review of Ecology and Systematics 30:51–81.

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout (Salvelinus fontinalis) populations in forested headwater streams. Hydrobiologia 515:203–213.

Hayes, J. W., N. F. Hughes, and L. H. Kelly. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. Ecological Modelling 207:171–188.

Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Johansen, M., J. M. Elliott, and A. Klemetsen. 2005. Relationships between juvenile salmon, *Salmo salar* L., and invertebrate densities in the River Tana, Norway. Ecology of Freshwater Fish 14:331–343.

Kaylor, M. J., B. J. VerWey, A. Cortes, and D. R. Warren. 2019. Drought impacts to trout and salamanders in cool, forested headwater ecosystems in the western Cascade Mountains, OR. Hydrobiologia 833:65–80.

Kelly-Quinn, M., and J. J. Bracken. 1990. A seasonal analysis of the diet and feeding dynamics of brown trout, Salmo trutta L., in a small nursery stream. Aquaculture Research 21:107–124.

Penaluna, B. E., J. B. Dunham, and H. V. Andersen. 2021. Nowhere to hide: The importance of instream cover for stream-living Coastal Cutthroat Trout during seasonal low flow. Ecology of Freshwater Fish 30:256–269.

Roni, P., K. Hanson, and T. Beechie. 2008. Global Review of the Physical and Biological Effectiveness of Stream Habitat Rehabilitation Techniques. North American Journal of Fisheries Management 28:856–890.

Rose, R., and A. Oliver. 2017. Limiting Factors in Mountain Stream Trout Habitat—Review of the Science.

Rosenfeld, J. S., J. Post, G. Robins, and T. Hatfield. 2007. Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat. Canadian Journal of Fisheries and Aquatic Sciences 64:755–767.

Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202–218.

Sabo, J. L., and G. B. Pauley. 1997. Competition between stream-dwelling cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*): effects of relative size and population origin. Canadian Journal of Fisheries and Aquatic Sciences 54:2609–2617.

Sheldon, K. A. 2010. Season-specific survival and growth rates of coastal cutthroat trout across a gradient of stream sizes in southwestern British Columbia. University of British Columbia.

Slaney, P. A., and T. G. Northcote. 1974. Effects of Prey Abundance on Density and Territorial Behavior of Young Rainbow Trout (*Salmo gairdneri*) in Laboratory Stream Channels. Journal of the Fisheries Research Board of Canada 31:1201–1209.

Warren, M., M. Dunbar, and C. Smith. 2015. River flow as a determinant of salmonid distribution and abundance: a review. Environmental Biology of Fishes 98.

White, S., C. Gowan, K. Fausch, J. Harris, and W. Saunders. 2011. Response of Trout Populations in Five Colorado Streams Two Decades after Habitat Manipulation. Canadian Journal of Fisheries and Aquatic Sciences 68:2057.

Wilzbach, M. 2011. Relative Roles of Food Abundance and Cover in Determining the Habitat Distribution of Stream-Dwelling Cutthroat Trout (Salmo clarki). Canadian Journal of Fisheries and Aquatic Sciences 42:1668–1672.

Appendices

Appendix 1: Procedures

Periphyton

- Materials: metal scrubbing brushes, plastic container, 20 mL plastic graduated cylinder, 100 mL plastic graduated cylinder, filter tower, hand pump for filtering, spray bottle with DI water, Nalgene with DI water for refilling spray bottle,

  pre-ashed GF/F filters (ashing is completed in muffle furnace 500C for 2 hours), foil squares, filter forceps, lab tape, Sharpie, ice pack and plastic bag for samples, data sheets, and pencil.
- Methods:

1. At each sampling location, select 3 similarly sized rocks from a riffle. More than 3 may be needed to generate a slurry of adequate size if the rocks are small.
2. In a shaded area, use the metal brush to scrub rock surface of all biofilm into the plastic container, rinsing biofilm off of rock with the spray bottle as necessary. Use as little water as possible in order to avoid diluting the sample.
3. After scrubbing each rock, trace their outline on a Rite in the Rain blank data sheet, holding the pencil perpendicular to the paper. Label each tracing with the Site, meter, rock number, and date. When finished, do not place rocks back in stream.
4. Pour slurry from the plastic container into the 100 mL graduated cylinder, using spray bottle of DI water to rinse if needed. Record the total slurry volume on the data sheet.
    a. If you are not filtering the slurry in the field (i.e.: bringing it back to the lab), store slurry into a dark container to protect it from light.
5. Use forceps to place a filter onto the vacuum pump and assemble pump to seal it in place.
6. Homogenize the slurry, then pour a subsample into the 20 mL graduated cylinder (approximately 15mL). Three subsamples will be used, so make sure there will be enough slurry to do all three.
7. Record the volume of the subsample, then pour the subsample into the filter tower and pull the liquid through using the hand pump.

8. Disassemble the filter tower and remove the filter from the vacuum pump using forceps. Fold the filter in half (making a taco shape), and then wrap it in foil. When folding the filter, ensure that nothing touches it but the forceps and foil, and that the sample is not disturbed. The sample should be folded exactly in half so that none of it is touching anything other than the foil.
9. Label a piece of lab tape with the site, date, meter, and subsample volume, and stick on the outside of the folded foil. Store folded foil flat on the icepack and move to cooler/freezer as soon as possible.
10. Repeat steps 5-9 two more times to collect a total of three subsamples.

Wetted width, bankfull width, depths

- Materials: Meter tape, laser distance meter, ruler, datasheets, clipboard, pencil
- Method:

  Bankfull Width: Bankfull width measures the distance between the stream bank during high flow events, and can be identified based on vegetation boundaries, moss lines, changes in substrate, etc. Use the laser distance meter to measure the distance between the high flow point of each banks, running perpendicular to the stream.

  Wetted width: Wetted width measures the distance across the stream at the time of the sampling event. Use the laser distance meter to measure the distance between the water's edge on each side of the stream, running perpendicular across the stream. If the channel is split by a feature more than 40% of the total width, note this down and take measurements as if it were 2 transects.

  Depth: Five depths are collected at each sampling point, and are taken at consistent intervals across the stream (i.e.: if the stream was divided into 5 even sections, a sample would be taken at the center of each section). Use the ruler to measure straight down into the water, but do not push the ruler into the sediment.

Canopy cover

- Canopy cover was measured using a densiometer at eight locations in each stream, at locations of consistent intervals apart.
- Materials: Densiometer, compass, datasheets, clipboard, pencil
- Methods:

  1. Use the compass to find North and orient yourself so you are facing that direction.
  2. Hold the densitometer at waist height and adjust so it is level.
  3. Mentally divide each of the squares on the densiometer into four smaller squares and imagine that there is a dot in the middle of each of the smaller squares. Count the number of “dots” that are located in open sky and record the number.
  4. Repeat measurement for facing East, South, and West.

Pool area & depths

- The area and depths of pools within the fishing reach were measured at all pool locations within the fishing reach.
- Materials: Laster distance meter, rulers or metersticks, datasheets, pencil, clipboard
- Methods:

  1. Going through the entire stream reach, recognize pools as areas with low velocity and turbulence and can act as fish habitat. Record the approximate meter location of each pool.
  2. Measure the two longest perpendicular axes of the pool using the laser distance meter, and record.
  3. Use the ruler. Or meterstick to measure the maximum depth of the pool, as well as the outflow depth.
  4. Repeat steps 1-3 along the entire fishing reach.

Electrofishing

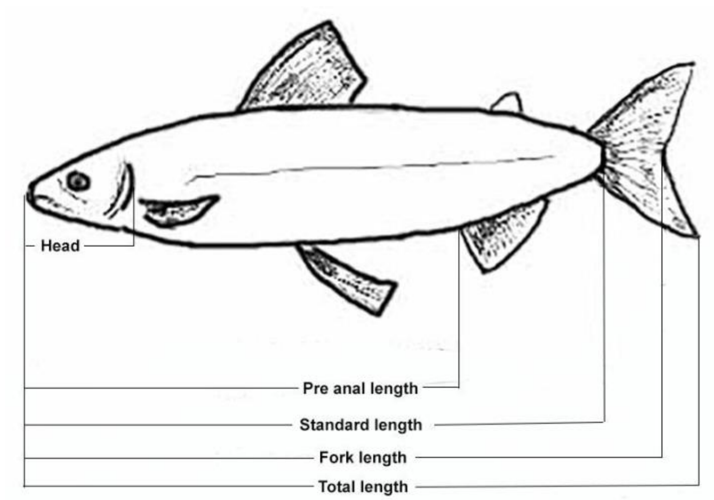
- Materials: backpack electrofisher (Smith-Root Model LR-20B), nets (of various sizes and handle lengths), block nets, four 5 gallon buckets, 5 bucket aerators, measuring board, scale, weight boat, AquiS (in dark bottle), PIT tags, PIT tag gun, PIT tag reader, datasheets, pencil, clipboard
- Methods:
  1. Ensure that he electrofisher batteries are fully charged ahead of sampling. Attach the battery to the electrofisher.
  2. Set up block nets at each end of the fishing reach to keep vertebrates within the reach. Remove all loggers from the water within the fishing reach.
  3. Set up a processing station on the streambank for when you are done fishing. It is usually easiest to set up around the middle. Of the fishing reach, so you can swap buckets while fishing if needed.
     a. The station should have a recovery bucket equipped with stream water, floating vegetation, and at least one aerator, the digital scale (unlocked, powered on, located on a flat surface within a tub for protection, and holding a weigh boat), a measureboard, datasheets, clipboard, and pencils, a batch of AquiS concentrated in a bucket of stream water and an aerator for sedating fish, PIT tags, a PIT tag gun, and a PIT tag reader.
  4. Use the quick-start settings for the Smith-Root Model LR-20B electrofisher, which are a waveform of 30Hz and a 12% duty cycle. The average power output should be 25 W, so voltage should be set around 250V, although this may need to be adjusted based on stream conductivity.
  5. Turn on the electrofisher and set the time to zero before sampling begins. Start at the downstream end of the fishing reach, above the lower block net. One person will wear and control the electrofisher, one person will carry a half-full bucket of stream water to deposit vertebrates into, and one or more people will carry nets to catch fish and vertebrates.

Vertebrates should be deposited into the bucket immediately, and the bucket should be equipped with an aerator and contain some floating vegetation to provide cover.

   a. A good setup is having the person wearing the electrofisher to be standing in the middle of the stream, with one netter on each side of them, and then the person carrying the bucket either ahead of them or behind them, depending on the layout of the stream.
   b. Multiple buckets may be used if one gets too crowded, or if adults and fry need to be separated. A separate bucket should also be used to hold any neotenes, as they will prey on smaller fish and salamanders.

6. Fish up the stream until you hit the upstream block net. Ensure that all habitat, is searched thoroughly, but do not overexpose fish to electricity.
7. After the first pass is completed, record the date, meter, and site details, along with the length of time spent fishing (as shown on the electrofisher) and the settings used (V, amp, duty cycle, Hz, amp). Cover the bucket of fish with a lid or clipboard and leave in a shady part of the processing station.
8. Repeat steps 4- 7 two more times for a total of three passes. Use a new bucket (or set of buckets) for each pass, and keep thee catches of each pass separate from each other.
9. After all three passes are complete, you can begin processing them. Process the animals from one pass at a time. Use an aquarium net to remove a few fish from the sampling bucket, and place them in the solution of AquiS. After a minute or two, they will turn on their sides, indicating that thee anesthetic is taking effect.
   a. Larger fish
10. Once a fish is adequately anesthetized for handling, remove the fish from the solution, and use the measure board to measure its fork length and total length, and use the scale to

measure its weight. Record all measurements on the datasheet, and place fish in the recovery bucket.



11. Repeat steps 9-10 until all of the animals from the sample (pass) have been processed, then repeat with each of the other passes.
12. After all the fish have been measured, they can be moved from the recovery bucket back to the stream. They should be evenly distributed throughout the stream, and neotenes should be returned to the pool/location where they were found.

Appendix 2: Correlation Matrices

Table 1A: Correlation values for adult cutthroat density

	Lower-flow year (2021)		Higher-flow year (2022)	
	Correlation	p-value	Correlation	p-value
Total Pool Area	-0.031072938	0.90905068	-0.135502966	0.61681929
Max. Pool Depth	-0.099295577	0.71446211	-0.149430332	0.58070679
Log Canopy Cover	0.207562581	0.44049308	-0.013476862	0.96049187
Ash-Free Dry Mass	-0.285912696	0.28304999	0.027945617	0.91817406
Temperature	0.072247686	0.79031982	0.167788309	0.53450777
EPT	-0.083397294	0.7587944594	-0.066666460	0.8062190885

Table 1A: *Correlation values for adult cutthroat density, as shown in correlation heatmap*

Table 2A: Correlation values for adult cutthroat biomass density

	Lower-flow year (2021)		Higher-flow year (2022)	
	Correlation	p-value	Correlation	p-value
Total Pool Area	0.283190090	0.2878608146	-0.299881106	0.2591344979
Max. Pool Depth	-0.096684332	0.7216891440	0.021144425	0.9380469049
Log Canopy Cover	0.141123469	0.6021404380	-0.130512723	0.6299673336
Ash-Free Dry Mass	-0.286345095	0.2822904232	0.253559475	0.3433447982
Temperature	0.245094558	0.3602349652	0.234883480	0.3812119889
EPT	0.118221423	0.6627924540	-0.078958017	0.7713067037

Table 2A: *Correlation values for adult cutthroat biomass density, as shown in correlation heatmap*

Table 3A: Correlation values for young-of-year density

	Lower-flow year (2021)		Higher-flow year (2022)	
	Correlation	p-value	Correlation	p-value
Total Pool Area	-0.054255869	0.8418209356	0.235444577	0.3800423533
Max. Pool Depth	0.323272727	0.2219620895	-0.040264135	0.8823026370
Log Canopy Cover	-0.156250131	0.5633517453	-0.023501644	0.9311547472
Ash-Free Dry Mass	-0.098965701	0.7153738547	-0.168035881	0.5338962161
Temperature	0.2179335	0.4174591414	-0.168035881	0.5338962161
EPT	-0.247499644	0.3553897157	0.154377706	0.5680945062

Table 3A: Correlation values young-of-year density, as shown in correlation heatmap

Table 4A: Correlation values for young-of-year biomass density

	Lower-flow year (2021)		Higher-flow year (2022)	
	Correlation	p-value	Correlation	p-value
Total Pool Area	0.009712189	0.9715232	0. 039661974	0.8840517
Max. Pool Depth	0.116972590	0.6661612	-0.108967965	0.6878940
Log Canopy Cover	-0.093498213	0.7305372	0.001039972	0.9969502
Ash-Free Dry Mass	-0.085794197	0.7520618	-0.137877746	0.6106002
Temperature	-0.409167055	0.1155519	-0.058589393	0.8293533
EPT	-0.054640591	0.8407126	0.342889322	0.1935515

Table 4A: *Correlation values for young-of-year biomass density, as shown in the correlation heatmap*

Appendix 3: Complete AICc tables

Table 5A: Complete AICc results for adult cutthroat density during the lower-flow year (2021)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	-26.32	0	0.31	0.31	15.62
AFDM	3	-24.6	1.71	0.13	0.45	16.3
CAN	3	-23.94	2.37	0.1	0.54	15.97
MMD	3	-23.4	2.92	0.07	0.61	15.7
EPT	3	-23.35	2.97	0.07	0.69	15.68
TMP	3	-23.32	2.99	0.07	0.76	15.66
PLA	3	-23.25	3.06	0.07	0.82	15.63
AFDM + EPT	4	-21.11	5.2	0.02	0.85	16.37
AFDM + EPT + CAN	4	-21.11	5.2	0.02	0.87	16.37
AFDM + TMP	4	-21.03	5.29	0.02	0.89	16.33
AFDM + MMD	4	-21	5.31	0.02	0.91	16.32
CAN + MMD	4	-20.55	5.76	0.02	0.93	16.09
CAN + PLA	4	-20.43	5.88	0.02	0.95	16.03
CAN + TMP	4	-20.36	5.96	0.02	0.96	16
TMP + EPT	4	-19.77	6.55	0.01	0.98	15.7
PLA + TMP	4	-19.72	6.6	0.01	0.99	15.68
PLA + EPT	4	-19.71	6.6	0.01	1	15.68
PLA + TMP + MMD	5	-15.47	10.85	0	1	15.73
global	8	2.55	28.87	0	1	17.01

Table 5A: Results of AIC analysis of linear models assessing relationships between adult trout per m and stream characteristics in summer 2021.
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 6A: Complete AIC results for adult cutthroat density during the higher-flow year (2022)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	-34.47	0	0.35	0.35	19.7
TMP	3	-31.85	2.62	0.09	0.44	19.92
MMD	3	-31.75	2.72	0.09	0.53	19.88
PLA	3	-31.69	2.78	0.09	0.62	19.84
EPT	3	-31.46	3.01	0.08	0.7	19.73
AFDM	3	-31.4	3.06	0.08	0.77	19.7
CAN	3	-31.39	3.07	0.07	0.85	19.7
AFDM +TMP	4	-28.58	5.89	0.02	0.87	20.11
PLA + TMP	4	-28.5	5.97	0.02	0.88	20.07
TMP + EPT	4	-28.28	6.18	0.02	0.9	19.96
CAN + TMP	4	-28.23	6.24	0.02	0.91	19.93
AFDM +MMD	4	-28.19	6.27	0.02	0.93	19.92
CAN + MMD	4	-28.14	6.33	0.01	0.94	19.89
CAN + PLA	4	-28.05	6.41	0.01	0.96	19.85
PLA + EPT	4	-28.05	6.42	0.01	0.97	19.84
AFDM + EPT	4	-27.83	6.64	0.01	0.99	19.73
AFDM + EPT + CAN	4	-27.83	6.64	0.01	1	19.73
PLA + TMP + MMD	5	-24.34	10.13	0	1	20.17
global	8	-4.48	29.99	0	1	20.53

***Table 6A:** Results of AIC analysis of linear models assessing relationships between adult trout per m and stream characteristics in summer 2022.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 7A: Complete AIC results for adult cutthroat biomass density during the lower-flow year (2021)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	31.66	0	0.27	0.27	-13.37
AFDM	3	33.37	1.71	0.12	0.39	-12.69
PLA	3	33.4	1.74	0.11	0.5	-12.7
TMP	3	33.75	2.09	0.1	0.6	-12.88
CAN	3	34.42	2.76	0.07	0.67	-13.21
EPT	3	34.52	2.85	0.07	0.74	-13.26
MMD	3	34.59	2.93	0.06	0.8	-13.3
PLA + TMP	4	36.31	4.65	0.03	0.83	-12.34
AFDM +TMP	4	36.7	5.03	0.02	0.85	-12.53
AFDM + EPT	4	36.79	5.13	0.02	0.87	-12.58
AFDM + EPT + CAN	4	36.79	5.13	0.02	0.89	-12.58
TMP + EPT	4	36.89	5.23	0.02	0.91	-12.63
CAN + PLA	4	36.95	5.29	0.02	0.93	-12.66
AFDM + MMD	4	36.98	5.31	0.02	0.95	-12.67
PLA + EPT	4	37.04	5.37	0.02	0.97	-12.7
CAN + TMP	4	37.14	5.47	0.02	0.98	-12.75
CAN + MMD	4	37.85	6.19	0.01	1	-13.11
PLA + TMP + MMD	5	40.42	8.75	0	1	-12.21
global	8	60.54	28.88	0	1	-11.99

Table 7A: *Results of AIC analysis of linear models assessing relationships between adult trout biomass per m and stream characteristics in summer 2021.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 8A: Complete AIC results for adult cutthroat biomass density during the higher-flow year (2022)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	33.32	0	0.25	0.25	-14.2
PLA	3	34.89	1.57	0.12	0.37	-13.45
AFDM +TMP	4	34.93	1.61	0.11	0.48	-11.65
AFDM	3	35.33	2.01	0.09	0.58	-13.67
TMP	3	35.49	2.17	0.09	0.66	-13.74
CAN	3	36.12	2.8	0.06	0.73	-14.06
EPT	3	36.3	2.98	0.06	0.78	-14.15
MMD	3	36.39	3.07	0.05	0.84	-14.2
PLA + TMP	4	37.6	4.28	0.03	0.87	-12.98
CAN + PLA	4	38.43	5.11	0.02	0.89	-13.4
PLA + EPT	4	38.47	5.15	0.02	0.91	-13.42
CAN + TMP	4	38.72	5.4	0.02	0.92	-13.54
AFDM + EPT	4	38.93	5.61	0.02	0.94	-13.65
AFDM + EPT + CAN	4	38.93	5.61	0.02	0.96	-13.65
AFDM + MMD	4	38.93	5.61	0.02	0.97	-13.65
TMP + EPT	4	39.02	5.7	0.01	0.99	-13.69
CAN + MMD	4	39.76	6.44	0.01	1	-14.06
PLA + TMP + MMD	5	41.66	8.34	0	1	-12.83
global	8	56.55	23.23	0	1	-9.99

Table 8A: Results of AIC analysis of linear models assessing relationships between adult trout biomass per m and stream characteristics in summer 2022.

Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 9A: Complete AIC results for young-of-year density during the lower-flow year (2021)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	9.22	0	0.27	0.27	-2.15
MMD	3	10.53	1.31	0.14	0.41	-1.27
EPT	3	11.29	2.07	0.1	0.51	-1.64
TMP	3	11.52	2.3	0.09	0.6	-1.76
CAN	3	11.91	2.68	0.07	0.67	-1.95
AFDM	3	12.14	2.92	0.06	0.73	-2.07
PLA	3	12.25	3.03	0.06	0.79	-2.13
CAN +MMD	4	13.52	4.29	0.03	0.82	-0.94
TMP + EPT	4	13.62	4.4	0.03	0.85	-0.99
AFDM + MMD	4	13.69	4.47	0.03	0.88	-1.03
AFDM +TMP	4	14.36	5.13	0.02	0.9	-1.36
AFDM +EPT	4	14.73	5.51	0.02	0.92	-1.55
AFDM + EPT + CAN	4	14.73	5.51	0.02	0.94	-1.55
CAN +TMP	4	14.84	5.61	0.02	0.95	-1.6
PLA + EPT	4	14.86	5.64	0.02	0.97	-1.61
PLA + TMP	4	15.15	5.93	0.01	0.98	-1.76
CAN +PLA	4	15.54	6.31	0.01	1	-1.95
PLA + TMP + MMD	5	17.82	8.6	0	1	-0.91

Table 9A: *Results of AIC analysis of linear models assessing relationships between YOY density per m and stream characteristics in summer 2021.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 10A: Complete AIC results for young-of-year density during the higher-flow year (2022)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	-7.95	0	0.33	0.33	6.44
PLA	3	-5.79	2.16	0.11	0.44	6.89
TMP	3	-5.33	2.62	0.09	0.53	6.67
EPT	3	-5.26	2.69	0.09	0.62	6.63
AFDM	3	-4.98	2.97	0.07	0.69	6.49
MMD	3	-4.9	3.05	0.07	0.76	6.45
CAN	3	-4.88	3.07	0.07	0.84	6.44
PLA + TMP	4	-2.6	5.35	0.02	0.86	7.12
CAN + PLA	4	-2.23	5.72	0.02	0.88	6.93
PLA + EPT	4	-2.21	5.74	0.02	0.9	6.92
TMP + EPT	4	-2.09	5.86	0.02	0.91	6.86
AFDM + EPT	4	-1.79	6.16	0.02	0.93	6.71
AFDM + EPT + CAN	4	-1.79	6.16	0.02	0.94	6.71
AFDM + TMP	4	-1.7	6.25	0.01	0.96	6.67
CAN + TMP	4	-1.7	6.25	0.01	0.97	6.67
AFDM + MMD	4	-1.41	6.54	0.01	0.99	6.52
CAN + MMD	4	-1.28	6.67	0.01	1	6.46
PLA + TMP + MMD	5	1.5	9.45	0	1	7.25
global	8	21.94	29.89	0	1	7.32

Table 10A: Results of AIC analysis of linear models assessing relationships between YOY density per m and stream characteristics in summer 2022.
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 11A: Complete AIC results for young-of-year biomass density during the lower-flow year (2021)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	9.22	0.00	0.27	0.27	-2.15
MMD	3	10.53	1.31	0.14	0.41	-1.27
EPT	3	11.29	2.07	0.1	0.51	-1.64
TMP	3	11.52	2.30	0.09	0.6	-1.76
CAN	3	11.91	2.68	0.07	0.67	-1.95
AFDM	3	12.14	2.92	0.06	0.73	-2.07
PLA	3	12.25	3.03	0.06	0.79	-2.13
CAN + MMD	4	13.52	4.29	0.03	0.82	-0.94
TMP + EPT	4	13.62	4.40	0.03	0.85	-0.99
AFDM + MMD	4	13.69	4.47	0.03	0.88	-1.03
AFDM + TMP	4	14.36	5.13	0.02	0.9	-1.36
AFDM + EPT	4	14.73	5.51	0.02	0.92	-1.55
AFDM + EPT + CAN	4	14.73	5.51	0.02	0.94	-1.55
CAN + TMP	4	14.84	5.61	0.02	0.95	-1.6
PLA + EPT	4	14.86	5.64	0.02	0.97	-1.61
PLA + TMP	4	15.15	5.93	0.01	0.98	-1.76
CAN + PLA	4	15.54	6.31	0.01	1	-1.95
PLA + TMP + MMD	5	17.82	8.60	0	1	-0.91
global	8	35.8	25.86	0	1	0.74

Table 11A: *Results of AIC analysis of linear models assessing relationships between YOY biomass density per m and stream characteristics in summer 2021.*
Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature

Table 12A: Complete AIC results for young-of-year biomass density during the higher-flow year (2022)

Model	K	AIC	Delta AIC	AIC Wt.	Cum. Wt.	LL
Null	2	-7.95	0	0.33	0.33	6.44
PLA	3	-5.79	2.16	0.11	0.44	6.89
TMP	3	-5.33	2.62	0.09	0.53	6.67
EPT	3	-5.26	2.69	0.09	0.62	6.63
AFDM	3	-4.98	2.97	0.07	0.69	6.49
MMD	3	-4.9	3.05	0.07	0.76	6.45
CAN	3	-4.88	3.07	0.07	0.84	6.44
PLA + TMP	4	-2.6	5.35	0.02	0.86	7.12
CAN + PLA	4	-2.23	5.72	0.02	0.88	6.93
PLA + EPT	4	-2.21	5.74	0.02	0.9	6.92
TMP + EPT	4	-2.09	5.86	0.02	0.91	6.86
AFDM + EPT	4	-1.79	6.16	0.02	0.93	6.71
AFDM + EPT + CAN	4	-1.79	6.16	0.02	0.94	6.71
AFDM + TMP	4	-1.7	6.25	0.01	0.96	6.67
CAN + TMP	4	-1.7	6.25	0.01	0.97	6.67
AFDM + MMD	4	-1.41	6.54	0.01	0.99	6.52
CAN + MMD	4	-1.28	6.67	0.01	1	6.46
PLA + TMP + MMD	5	1.5	9.45	0	1	7.25
global	8	21.94	29.89	0	1	7.32

***Table 12A**: Results of AIC analysis of linear models assessing relationships between YOY biomass density per m and stream characteristics in summer 2022.*

Abbreviations: AFDM= mean ash-free dry mass, CAN= mean canopy cover, MMD = mean maximum pool depth, PLA= total pool area, TMP = mean summer temperature