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RESEARCH ARTICLE

Stream hydrology and a pulse subsidy shape patterns of fish foraging

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Abstract

1. Pulsed subsidy events create ephemeral fluxes of hyper-abundant resources that can shape annual patterns of consumption and growth for recipient consumers. However, environmental conditions strongly affect local resource availability for much of the year, and can heavily impact consumer foraging and growth patterns prior to pulsed subsidy events. Thus, a consumer's capacity to exploit pulse subsidy resources may be influenced by antecedent environmental conditions, but this has rarely been shown in nature and is unknown in aquatic ecosystems.
2. Here, we sought to understand the importance of hydrologic variation and a salmon pulse subsidy on the foraging and growth patterns of two stream salmonids in a coastal southeast Alaska drainage.
3. To do this, we sampled fish stomach contents at a high temporal frequency (daily–weekly measurements) and analyzed fish consumption rates in relation to streamflow and pulse subsidy resource availability. We then explored the influence of interannual hydrologic variation on access to pulse subsidy resources (i.e. whether fish exceeded an egg consumption gape limit) in a bioenergetic simulation.
4. Prior to Pink Salmon spawning, Dolly Varden and Coho Salmon displayed distinct and nonlinear flow-foraging relationships, where forage for both species consisted primarily of macroinvertebrates. During this time period, consumption maxima coincided with baseflow and the highest observed flow conditions, and consumption minima were observed at severe low-water and intermediate flow values. After salmon spawning began, forage was not significantly related to flow and consisted primarily of salmon eggs. Further, consumption rates increased overall, and foraging patterns did not appear to be affected by flow in either species. Bioenergetic simulations revealed that patterns of interannual hydrologic variation may shift Coho Salmon growth trajectories among years.
5. Together, our results suggest that access to marine pulse subsidy resources may depend on whether antecedent hydrologic conditions are suitable for juvenile salmonids to grow large enough to consume salmon eggs by the onset of spawning.

KEYWORDS
antecedent conditions, ecohydrology, marine-derived resources, Pacific salmon, southeast Alaska

1 | INTRODUCTION

Temporal variability in abundance of food resources is known to shape patterns of consumer foraging and food-web structure in many ecosystems (Holling, 1973; Polis et al., 1997). Fluctuating environmental conditions frequently drive temporal patterns of local resource abundance, which in turn control rates of animal foraging (Jentsch & White, 2019; Yang et al., 2010). In some places, however, acute pulses of hyper-abundant external resources that operate independent of local environmental regimes can account for a disproportionately high percentage of energy intake by consumers (Bauer & Hoye, 2014; Yang et al., 2010). While these pulsed resource subsidies are known to exert great influence on patterns of recipient consumer foraging, the temporal scope of study around these inherently ephemeral events is often limited to the window of the event itself. However, the contextual importance of antecedent environmental conditions on patterns of consumer foraging and growth, and subsequent utilization of pulsed subsidy resources, remains largely unexplored (Subalusky & Post, 2019).

Stream hydrologic regimes can significantly influence species assemblages, food-web structure and foraging conditions for fish (Freeman et al., 2022; Poff et al., 1997; Power et al., 2015). Streamflow is also a primary mechanism by which locally derived aquatic and terrestrial macroinvertebrates are transported to, and consumed by, drift-foraging fish species (Fausch, 1984, 2014; Naman et al., 2016). Hydrologic conditions reflecting high, low and transitionary phases of streamflow may alter prey availability by inducing changes in fish foraging behaviour and patterns of invertebrate drift (Gibbins et al., 2007; Rossi et al., 2021; Suren & Jowett, 2006). However, aspects of this relationship, such as fish foraging during high- and low-flow extremes, are poorly understood (Piccolo et al., 2014). This knowledge gap is likely due to high variation in responses among stream types and fish species and difficulty observing fish during extreme hydrologic events (Freeman et al., 2022). Without easily generalizable patterns, high- and low-flow extremes are often assumed to provide poor foraging and growth conditions to resident fish. These assumptions are theoretically based on fish abandoning profitable foraging locations in favour of deep pool habitats to reduce stranding mortality risk at low flow (Lennox et al., 2019; Nagrodski et al., 2012; Sotiropoulos et al., 2006), as well as diminished prey detection from increased turbidity coupled with high energetic swimming costs at high flow (Fausch, 1984; Harvey & White, 2008). Despite uncertainties surrounding flow-foraging relationships, hydrologic regimes are often considered a key determinant of foraging and growth outcomes for drift-feeding fishes (Freeman et al., 2022; Lennox et al., 2019; Piccolo et al., 2014).

In riverine ecosystems that support anadromous Pacific salmon species (*Oncorhynchus* spp.), adult immigration and spawning create marine resource pulses, which can shape patterns of energy intake and growth by stream-dwelling fish (Armstrong et al., 2016; Scheuerell et al., 2007). High salmon egg consumption has been shown to more than double mid-summer body mass of stream-rearing juvenile Coho Salmon (*O. kisutch*) relative to unsubsidized predictions (Armstrong et al., 2010). Similarly, consumption of pulse subsidy resources by stream-dwelling Dolly Varden (*Salvelinus malma*) has accounted for entire annual energy surpluses among measured individuals (Armstrong & Bond, 2013). While salmon pulse subsidies clearly fuel energetic needs of recipient consumers, most research has focussed on consumer foraging and growth patterns when salmon are present and spawning (Armstrong et al., 2016; Bentley et al., 2012; Rinella et al., 2012), which may fail to recognize the importance of foraging conditions prior to the arrival of salmon. For example, juvenile salmonids must exceed a minimum gape-limited body size (approximately 70 mm for Coho Salmon) to access pulse subsidy resources (Armstrong et al., 2010), where fish below this size threshold are too small to consume salmon eggs. Antecedent hydrologic conditions may also shape early-season growth trajectories. Thus, suboptimal early-season streamflow patterns may limit fish foraging success and reduce growth rates to the point where a gape-limited size threshold is not exceeded, potentially restricting later access to salmon eggs. Here, we ask whether hydrologic environmental conditions antecedent to pulse subsidy events can facilitate consumer access to critically important marine-derived resources by influencing fish growth and gape limitation.

We examined how hydrologic conditions impact stream-rearing Coho Salmon and Dolly Varden foraging patterns before and after the onset of a pulsed salmon subsidy event. To do this, we collected fish stomach content samples at a high temporal frequency for 1 year within a hydrologically variable Alaskan stream that supports abundant spawning returns of Pink Salmon (*O. gorbuscha*). Our primary hypothesis was that streamflow variability and a salmon pulse subsidy would exert significant effects on prey consumption by juvenile salmonids. We then simulated Coho Salmon growth using discharge data from contrasting years to explore whether interannual hydrologic variation may alter Coho Salmon growth trajectories and impact subsidy resource utilization via slower growth and gape limitation to salmon eggs. Results of this research demonstrate the relative importance of hydrologic conditions in determining resource acquisition by consumers before and after an acute pulsed subsidy event, and support further exploration into whether antecedent hydrologic conditions mediate consumer access to salmon pulse subsidy resources.

2 | METHODS

2.1 | Study system

This study was carried out in a 400-m reach of upper Montana Creek, a small basin (9.5 km^2) in Juneau, Alaska (Figure 1). This catchment lies at the northern extent of the Pacific temperate rainforest in the coastal Gulf of Alaska (GOA), a hydrologically diverse landscape with abundant salmon-bearing watersheds (Sergeant et al., 2020). Streamflow in this basin is generated from large seasonal snowpack, usually present from November to May, and abundant rainfall from May to November. Land cover is primarily spruce-hemlock forest (85%) with some wetland cover (7%) and minimal land-use modification (Fellman et al., 2023). These characteristics generally reflect a postglacial watershed, a status many small mountain drainages in the region will trend towards in the coming decades (Sergeant et al., 2020). Streamflow in upper Montana Creek is strongly influenced by frequent rain events of sometimes high intensity, with recurring surges in discharge typically punctuated by rapid descents to base flow. The fish assemblage includes Coho, Pink, Chum (*O. keta*) and Chinook Salmon (*O. tshawytscha*), as well as Dolly Varden, Coastal Cutthroat (*O. clarkii*) and Rainbow Trout (*O. mykiss*), and Sculpins (*Cottus* spp.). However, juvenile Coho Salmon and Dolly Varden exist in the highest relative abundance. Here, and throughout the coastal GOA, Pink Salmon exhibit biennial spawning fluctuations associated with a fixed 2-year life history, resulting in abundances that are usually higher in odd relative to even years (Piston & Heinl, 2020).

2.2 | Data collection

Fish were sampled 45 times across a range of flow conditions (informed by National Weather Service (NWS) online flow data) from May to October 2021. In each sampling event, 4 to 10 fish traps baited with sterilized packaged salmon roe were deployed from 30 min to 12 h across the study reach. Trap numbers and soak durations (sampling effort) depended on the rate of fish capture. Seasonal changes

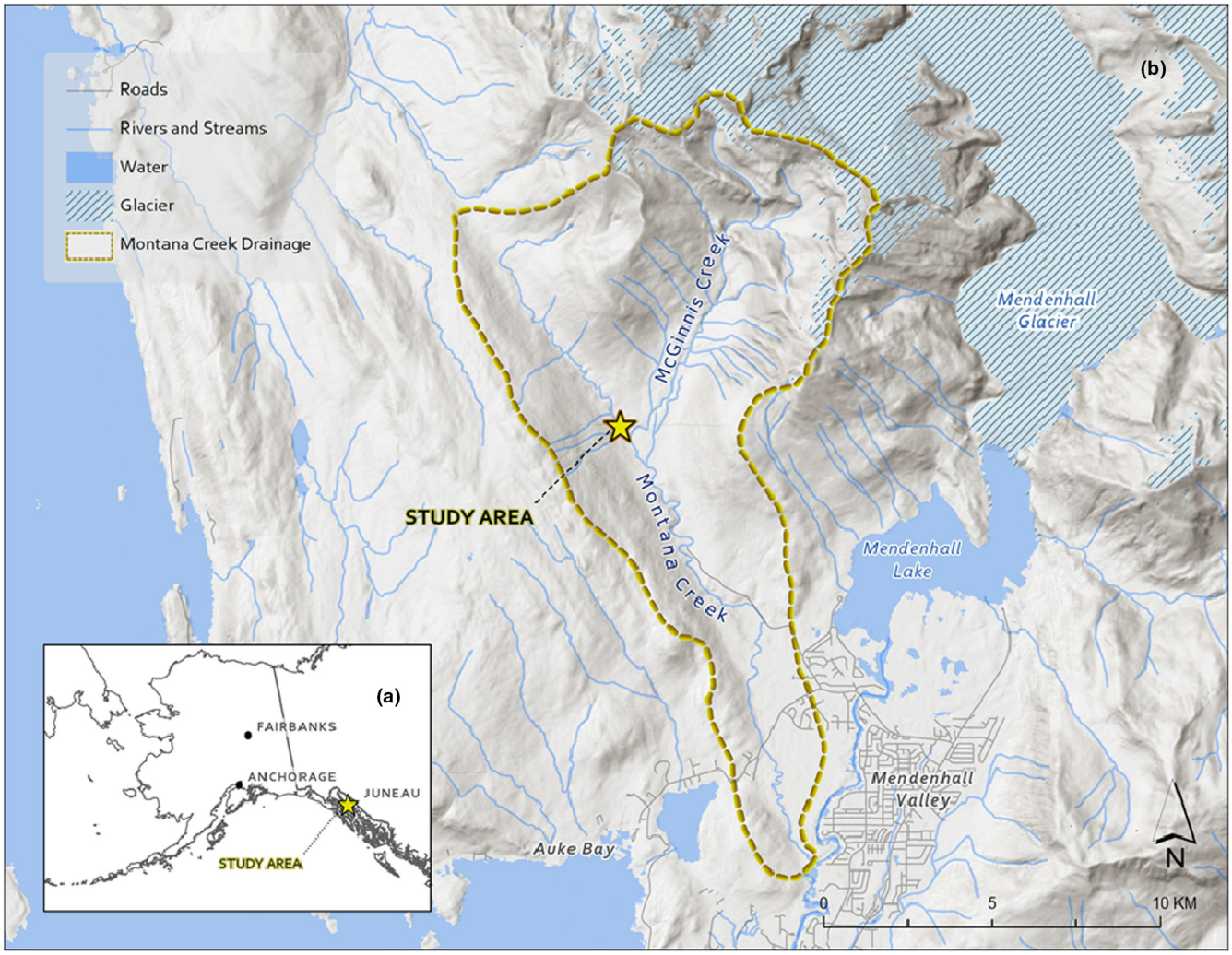

FIGURE 1 Map of study region. Position of the study location within Alaska is starred in inset (a). Boundaries of the study drainage are highlighted in yellow with location of study reach starred in inset (b).

in temperature, and consequent rates of fish metabolic activity, largely determined capture rates. All fish were anaesthetized in a 20 mg/L AQUI-S™ (AQUI-S New Zealand Ltd, Lower Hutt, New Zealand) bath, identified to species and measured for body mass (g) and total length (mm). Stomach content samples were collected at each sampling event using nonlethal gastric lavage from a subset target of 12 Coho Salmon and 6 Dolly Varden. However, actual diet sample numbers ranged from 0 to 22 per species depending on catch composition. Fish selected for diet sampling reflected the approximate distribution of body size and condition among captures. Gastric lavage was performed using a 100 mL syringe and rubber veterinary feeding needle above a 90 μm mesh sieve. Prey items were preserved in 95% ethanol after all stomach contents were extracted. Invertebrate drift data were also obtained from concurrent research within the study reach (Delbecq unpublished) and were used as a measure of drift biomass in subsequent statistical analyses. Methods for drift data collection in this study are thoroughly described in Fellman et al., 2023.

Stream discharge was collected using stage height (m) readings at 15-min intervals with an In-Situ Level Troll 500 pressure transducer combined with 19 discharge (m^3/s) measurements collected across a range of flow levels using a SonTek Flowtracker. Paired stage height-discharge measurements were subsequently used to calculate streamflow and generate a 15-min resolution hydrograph for the entire study period. Stream water temperature (°C) was measured on the same 15-min interval using a YSI EXO2 Sonde. Secondary measurements of temperature were also collected in each sampling event using a YSI handheld multiprobe (ProDSS) to ensure accuracy of Sonde measurements. Seasonal discharge was modelled annually from 2013 to 2021. This was done using discharge measurements collected from our study reach ($n = 27$) combined with historical discharge data from a NWS stream gauge 6 km downstream.

Pink Salmon spawning density was estimated four times with spawning count surveys. For this, Pink Salmon were counted by two observers within a 200-m reach. Stream surface area (m^2) was then calculated from reach length (m) and five evenly spaced channel width measurements (m), and mean fish count was standardized by stream channel surface area to estimate spawning fish density. Survey dates reflected the suspected first and last dates of Pink Salmon spawning and two intermediate points indicating peak spawning and carcass density.

2.3 | Laboratory methods

Prey items in fish diets were identified to the lowest practical taxonomic level using dissecting microscopes and dichotomous keys (Merritt & Cummins, 1996). Diet items were measured for length (mm), and ash-free dry masses (mg) were estimated using literature-based length–mass relationships for each taxa (Benke et al., 1999; Sabo et al., 2002; Wipfli, unpublished data). Prey biomasses were aggregated within diet samples to calculate total prey biomass consumed by individual fish. All invertebrates were assigned freshwater or terrestrial origins based on known life histories (Merritt & Cummins, 1996). Eggs, salmon flesh and early-life-stage salmon (fry and parr) were considered marine resources, since their nutrients are largely accumulated in the ocean.

2.4 | Analyses

Fish foraging patterns were analysed in a series of generalized additive models (GAMs) constructed using the 'mgcv' package (Wood, 2017) within RStudio (version 4.1.3; R Core Team, 2022). Although we initially explored modelling the entire time series, we subset the data into two periods (before/after Pink Salmon spawning began), because finer-scale temporal dynamics were largely masked by salmon spawning in the GAM encompassing the entire time series (see Supporting Information). The following model structure applied to the data subset from before Pink Salmon spawned tested the hypothesis that hydrologic variability would significantly affect prey consumption:

$$g(\text{Consumption}_i)^{-1} = \beta_0 + \text{Species}_i + s(\text{Temp}_i) + s_{\text{species}}(\text{Size}_i) + s_{\text{species}}(\text{Flow}_i) + s(\text{Drift}_i) + \varepsilon_i$$

Consumption was the average estimated ash-free dry biomass (mg) consumed across all fish for each day. A categorical term for species was included to account for differences in mean biomass consumed between Coho Salmon and Dolly Varden. Fifteen-min interval temperature (Temp; °C) and flow (m^3/s) data were averaged across 12 h prior to each sampling event. Flow was modelled as an interaction term with species (s_{species}) to account for species-specific foraging responses. Size was total length (mm) of the ith capture represented as an interaction term with species to account for size disparity between Coho Salmon and Dolly Varden. Drift was expressed as a concentration of estimated ash-free dry biomass of drifting prey at the time of sampling (mg/100m^3; Delbecq, unpublished). Temperature and fish size were smoothed control variables due to known nonlinear influences of temperature and size on fish metabolic rate and consumption. Species was a control variable and was included as a parametric term due to likely differences in mean biomass consumed between Coho Salmon and Dolly Varden, and to ensure interaction terms with species were centred with a mean zero effect. Flow and drift were candidate explanatory variables. None of the variables included in this model (Equation 1) were confounded with one another. Turbidity data were available, but were not included as an effect in the model due to high correlation with streamflow. A log-link function and Tweedie distributed errors (ε_i) were assumed. Smoothed variables $s()$ were estimated using cubic regression splines, and a maximum of four basis functions was specified to prevent overfitting. Initial explorations of estimating a smoothing penalty (via generalized cross-validation) suggested that the GAMs would overfit these data (i.e. fitting to noise rather than capturing patterns) and that a maximum of four basis functions was sufficient to capture existing nonlinearities (following methods described in Section 5.9; Wood, 2017). Given the common practices of other studies in fish ecology (Lehmann, 2002; Zucchetta

et al., 2010), and that these GAMs were constructed for prediction purposes (Sandman et al., 2008), this parameterization is likely appropriate. Akaike information criterion (AIC) was used for model selection, and an alpha value of $p=0.01$ was used to determine the statistical significance of smoothed terms, given that *p*-values from GAMs are approximate (Wood, 2017). The same formulation of the top-performing model fitted to the data subset from before Pink Salmon spawning was then applied to the data from after Pink Salmon spawning to facilitate comparability among models.

Diet composition was examined using proportions of prey type (aquatic, terrestrial, piscine and marine) across sample days and ecologically relevant categorical flow levels (low, moderate and high), which were qualitatively assigned based on interpretations from GAM outputs. Piscine prey encompassed any juvenile salmon found in fish diets and were stacked with marine prey in flow-foraging visualizations since nutrients in juvenile salmon are largely accumulated in the marine environment. For individual sample days, prey type proportions were calculated by species. Prey type proportions were also calculated by species for each flow level to evaluate compositional diet changes with flow. Temporal patterns of prey consumption were visualized using indices of size-adjusted stomach fullness, where ash-free dry biomasses of prey items were summed and divided by wet body mass of each fish to produce individual stomach fullness values, averaged by species across all fish on each sample day.

Impacts of interannual stream flow variation on age-1 Coho Salmon consumption and growth were modelled by year from 2013 to 2020 using predicted GAM relationships and historic flow data paired with a bioenergetic model to explore how hydrologic variability may impact Coho Salmon body size and their subsequent ability to consume salmon eggs. Mean daily discharge values from historical flow data between 1 May and 31 July in the years 2013–2020 were first input to the 'before Pink Salmon' GAM to produce predictions of daily ash-free dry-biomass prey consumption by juvenile Coho Salmon. Due to poor predictive capacity of GAMs outside the range of observed values, flows that were less than the 2021 minimum and greater than the 2021 maximum were constrained at the 2021 minimum and maximum flows (minimum: 0.3 m^3/s, maximum: 3.4 m^3/s) when predicting consumption. Cumulative consumption patterns in the years 2013–2021 were then compared with flow regime variation among years, which were visualized using annual hydrographs. Estimated daily consumption values from 2013 to 2021 were then used to simulate fish growth in the Wisconsin bioenergetic model (Deslauriers et al., 2017) parameterized for Coho Salmon (Stewart & Ibarra, 1991).

Predicted consumption from GAMs, mean daily flow from 2013 to 2021, empirical early-season Coho size data and 2021 thermal data were used to construct and parameterize a simulation to predict growth trajectories of age-1 Coho Salmon in the years 2013–2021. To do this, a theoretical maximum consumption (C_{max}) value (mg ash-free dry mass) was generated for the average-sized fish and adjusted for water temperature (Deslauriers et al., 2017). GAM-predicted consumption values based on mean daily stream flow were then divided by C_{max} to derive the proportion of C_{max} (pC_{max}). Daily pC_{max} values, mean daily water temperature data and starting Coho Salmon body size (observed on the first day of sampling) were used to simulate fish growth from 1 May to 31 July in the bioenergetic model. The pC_{max} time series was adjusted using a multiplication factor so that model outputs matched the observed age-1 Coho Salmon growth curve for 2021 (Figure S1). This approach resulted in realistic estimates of pC_{max} ($0.1<pC_{max}<0.3$), while retaining the flow-foraging patterns from the GAM. Prey was assumed to be comprised of 100% aquatic and terrestrial macroinvertebrates, with 25% indigestible by biomass (sensu Bellmore et al., 2013). To isolate the effect of interannual flow variation on fish growth, and because temperature data were not available every year, the 2021 thermal regime was used for all years in the bioenergetic simulation. Note, a downstream temperature monitoring site showed little interannual variation in thermal conditions (NWS), and no correlation between streamflow and water temperature was observed in 2021.

3 | RESULTS

3.1 | Trends in streamflow, stomach fullness and diet composition

The 2021 hydrograph included numerous high-flow events, particularly in the spring (1 May –21 June) and late summer/early fall (28 August–28 October), with a single extreme high flow in mid-August that peaked at 7.7 m^3/s (Figure 2a). Sustained low flows (typically less than 1.0 m^3/s) persisted for much of the summer (21 June–14 August), and consistent returns to low flow punctuated all surges in discharge outside this time. Pink Salmon were observed to begin spawning in the reach on 29 July and remained detectable through 14 September, with a peak spawning density of 0.175 fish/m^2 measured on 12 August (Figure 2b).

Stomach fullness trends were similar between species (Figure 2b), with exception of a few sampling dates (21 June, 13 July and 3 September). Mean stomach fullness increased from before salmon spawning (~0.002 g/g) to maximum values seen after (~0.02 g/g) in both species. Trends of aggregated diet composition across the study period showed that terrestrial and aquatic invertebrates were primarily consumed by both species prior to Pink Salmon spawning (Figure 2b,c). After spawning began, salmon eggs were as much as 94% of stomach content biomass consumed by Coho, and 98% of prey biomass consumed by Dolly Varden. This pattern continued for the rest of the study period, albeit at lower rates of consumption once Pink Salmon were no longer present.

3.2 | Environmental impacts on patterns of fish foraging

GAMs revealed significant flow-foraging relationships for both species, but was contingent on the presence or absence of Pink

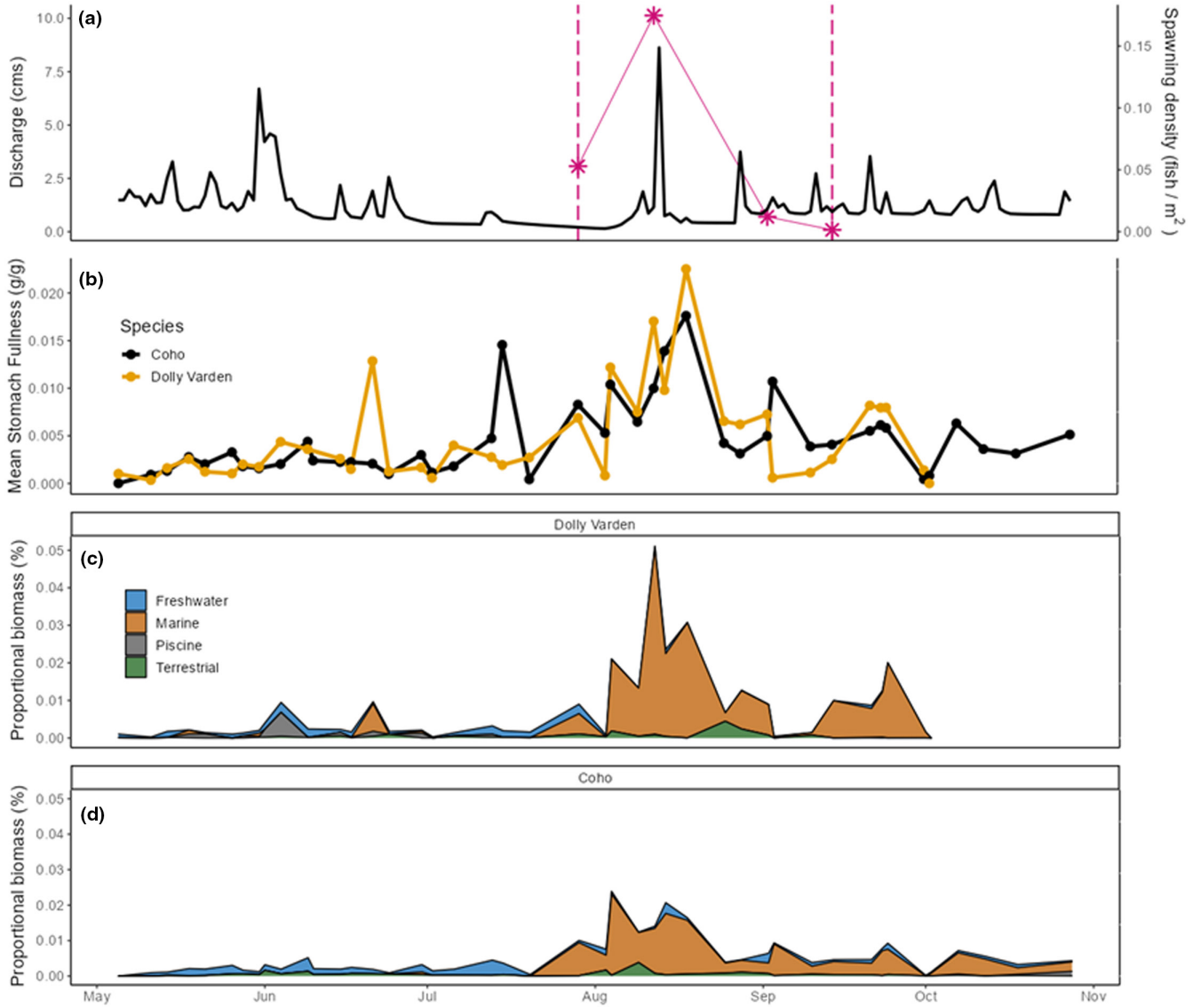

FIGURE 2 Time series of mean daily discharge and Pink Salmon spawning density (a), mean stomach fullness by fish species for each sampling date shown by points (b) and proportional consumption biomass with composition information for Dolly Varden (c) and Coho Salmon (Coho) (d). In panel (a), pink dotted lines delineate range of dates when Pink Salmon were observed spawning in the study reach and pink solid lines and asterisks indicate observed spawning densities.

Salmon. The top-performing GAM fit to data collected before Pink Salmon spawning showed significant effects of species ($p = 0.026$), temperature ($p < 0.01$), body size and flow (Table S1a). Body size (Coho: $p < 0.01$, Dolly: $p < 0.01$) and flow (Coho: $p < 0.01$, Dolly: $p < 0.01$) also had significant interactions with species, indicating species-specific foraging responses to these variables. For post-spawning data, the same model formulation revealed significant effects of temperature ($p < 0.01$), drift ($p < 0.01$) and body size (Coho: $p < 0.01$, Dolly: $p = 0.041$; Table S1b). Flow was not a significant predictor of consumption after salmon spawning began (Figure 3).

Predicted flow-foraging relationships prior to Pink Salmon spawning were nonlinear and species-distinct (Figure 3). For both fishes, lowest consumption was predicted to occur at the minimum flow extreme of 0.3 m^3/s (Dolly Varden: 4.01 mg, Coho: 3.02 mg). Consumption maxima of 14.39 mg for Dolly Varden and 12.77 mg for Coho occurred at low-flow values (Coho: 0.9 m^3/s, Dolly Varden: 0.9–1.17 m^3/s) for both species. This low-flow-foraging maximum was localized for Dolly Varden, but was the overall maximum for Coho Salmon within the observed flow range. Dolly Varden consumption declined under intermediate flow conditions to a minimum of 8.59 mg at 1.62 m^3/s and then increased dramatically towards maximum flow (3.4 m^3/s), with an overall consumption maximum (60.08 mg) predicted at the high-flow extreme. Coho consumption decreased to a local minimum of 3.77 mg through intermediate flows (2.3 m^3/s) and then increased to 7.36 mg towards the maximum flow (3.4 m^3/s). No statistically significant flow-foraging relationship

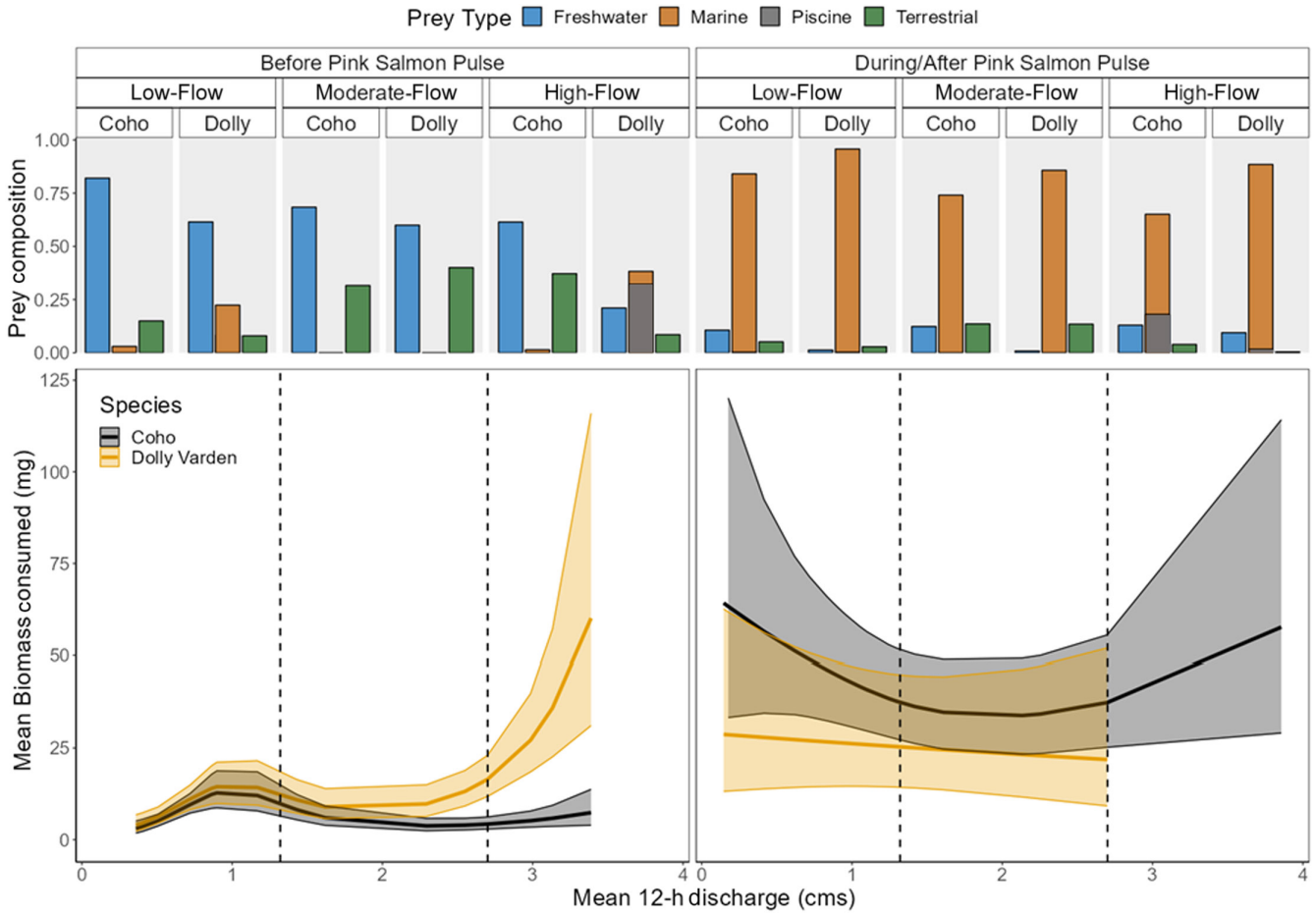

FIGURE 3 Four-panel figure of proportional prey composition (top) by categorical flow condition and species for periods before (left) and after (right) Pink Salmon spawning. Bottom panel shows GAM model outputs of estimated mean dry biomass consumed by species across the observed range of mean 12-h discharge. Dotted lines indicate approximate thresholds for categorical high-flow conditions. Actual thresholds are 1.5 (low to moderate flow) and 2.5 (moderate to high flow) m^3/s.

existed in either species for models fit to data after Pink Salmon spawning began.

3.3 | Prey composition changes with flow

Before Pink Salmon spawning, aggregate diet composition changed in both species across the range of observed flow values (Figure 3). At low flow, freshwater invertebrates comprised 81.2% of biomass consumed by Coho and 61.5% of biomass consumed by Dolly Varden. Relative consumption of aquatic prey declined with increasing flow to 61.4% for Coho and 21% for Dolly Varden at the highest observed flows. In contrast, terrestrial prey consumption increased from 14.9% for Coho and 7.9% for Dolly Varden at low flow, to 31.6% for Coho and 40% for Dolly Varden at moderate flow. This further increased to 37.2% at high flows for Coho. However, Dolly Varden increased consumption of marine/piscine prey to 32.8% at high flows, largely driven by increased piscivory of early-life-stage Salmonids. After Pink Salmon arrived, prey composition was dominated by salmon eggs, regardless of flow, and accounted for between 65% and 95.7% of biomass consumed across both species.

3.4 | Impacts of hydrologic variation on consumption and growth

Annual hydrographs from 2013 to 2021 showed substantial interannual variation in discharge (Figure 4a). Years 2013, 2020 and 2021 displayed flow values greater than the 2021 pre-salmon spawning minimum flow, and flow values often equalled or exceeded the GAM-based 0.9 m^3/s optimal foraging flow for Coho during the 1 May to 1 August period. In contrast, discharge in the years 2018 and 2019 was lower than the 2021 pre-salmon spawning minimum flow value, and flow values rarely equalled or exceeded the GAM-based 0.9 m^3/s optimal foraging flow for Coho during this same period.

Predicted trends of cumulative prey consumption for Coho reflected patterns in streamflow variation among years (Figure 4b). Generally, higher water years tended to increase overall consumption, and low-water years tended to lower overall consumption. Greatest cumulative consumption was predicted to have occurred in 2020, followed by 2021 and 2017. These corresponded to the 4th, 2nd and 3rd highest water years, respectively. Poorest cumulative consumption was predicted for 2018 followed by 2019, the lowest and second lowest water years. Predicted cumulative consumption

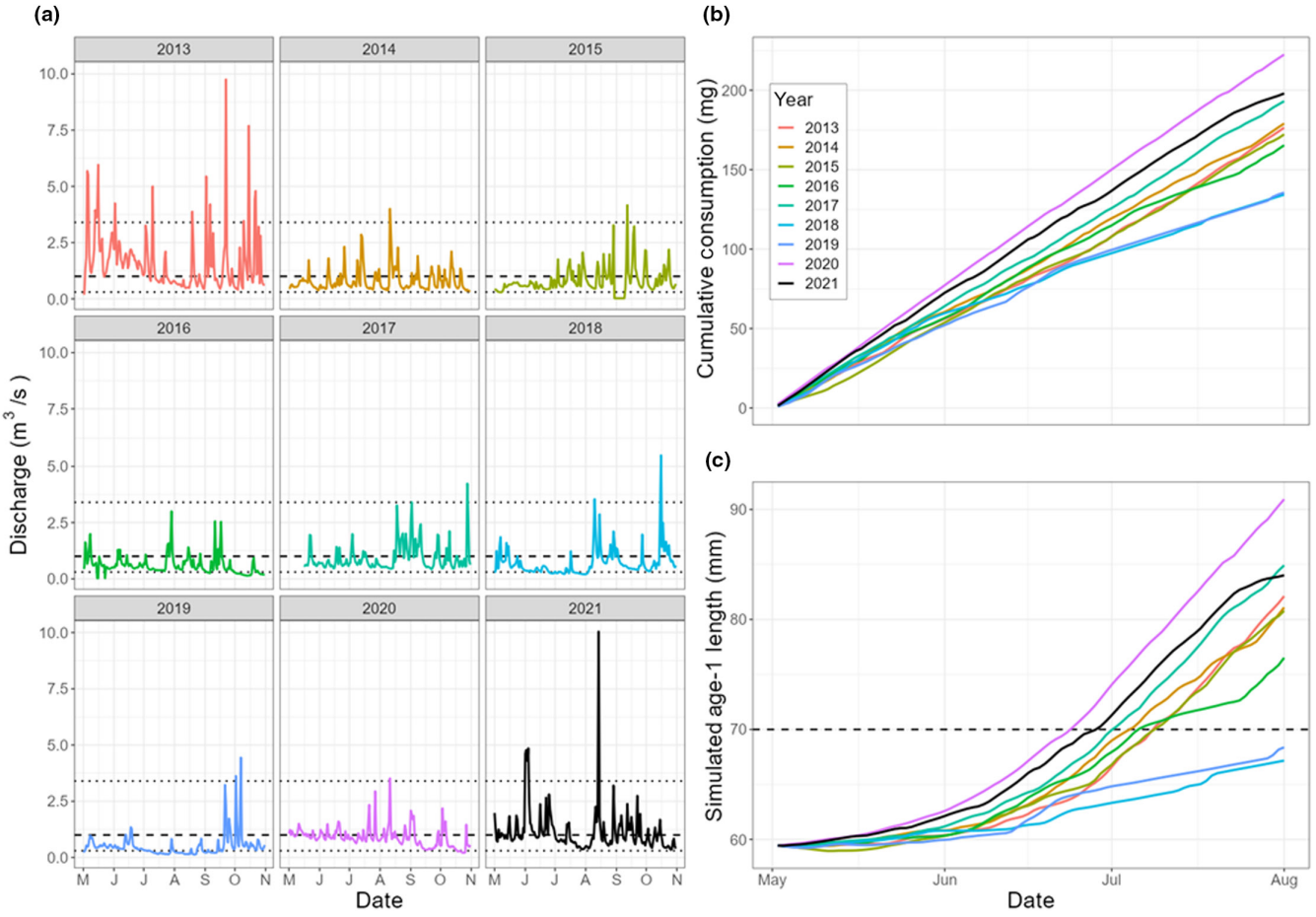

FIGURE 4 Three-panel plot of exceedance probabilities for observed mean daily discharge values among years (a), predicted cumulative consumption (b) and bioenergetically simulated growth trajectories (c). In panel (a), horizontal dotted lines represent maximum and minimum observed flow input to the GAM before Pink Salmon spawned, and the dashed solid line indicates the approximate optimal flow for Coho consumption. In panel (c), horizontal the dashed line indicates Coho gape limit required to consume salmon eggs.

for the average-sized Coho by the end of July was 65.7% greater in the highest water year (2020; consumption = 222.5 mg) compared with the lowest water year (2018; consumption = 134.1 mg).

Bioenergetic simulations of growth revealed stark differences in age-1 Coho size among years (Figure 4c). Trends of predicted size through time coincided with patterns seen in predicted annual cumulative consumption. In the years 2020, 2017 and 2021, Coho displayed the highest growth rates and reached the largest respective body sizes seen in the simulation (90.9, 84.9 and 84.1 mm). In contrast, the three lowest water years (2018, 2019 and 2016) produced the smallest predicted end-of-July body sizes (66.8, 68.1 and 75.8 mm). The difference in end-of-July body size between the highest (2020) and lowest (2018) growth years was 36.1%, and Coho were not predicted to reach a size large enough to consume salmon eggs in 2018 or 2019 owing to suboptimal early-season hydrologic conditions.

4 | DISCUSSION

Streamflow and salmon spawning exerted significant, but temporally discrete, influences on observed foraging patterns of juvenile Coho Salmon and Dolly Varden in a small coastal Alaska watershed (Figure 3). Fish foraging exhibited a strong and nonlinear relationship with flow prior to the pulsed salmon subsidy, but was unrelated to flow when salmon were present. Outcomes of bioenergetic simulations supported field observations and suggested that hydrologic variation among years has the potential to induce foraging and growth trajectory shifts in Coho, with likely consequences for marine-derived resource assimilation from the ensuing pulsed subsidy event (Figure 4). We establish the relative importance of local environmental conditions (streamflow) and a pulsed salmon subsidy in shaping fish foraging patterns. Broadly, these findings suggest that antecedent environmental conditions may facilitate temporal matches/mismatches between pulse subsidies and the ability of consumers to utilize them.

Modelled flow-foraging relationships (Figure 3) deviated from general assumptions of how streamflow influences fish foraging, particularly in Dolly Varden. Conventional theory assumes that optimal foraging occurs at low-to-moderate flows, with general declines in consumption as water velocity and turbidity increase with streamflow (Fausch, 1984, 2014; Harvey & White, 2008; Piccolo et al., 2014). However, our results suggest a more nuanced and

nonlinear flow-foraging relationship and the potential for multiple foraging maxima and minima within the range of potential flow conditions. As flow increased, foraging success of both species initially increased to a low-flow maximum. This maximum represented the highest consumption observed in Coho Salmon, but represented a localized consumption maximum for Dolly Varden. Consumption then decreased to a moderate-flow minimum for both species and then again increased towards the highest observed flows. This consumption increase was small for Coho Salmon, but reflected the highest rates of consumption observed for Dolly Varden.

Such nonlinear foraging responses are likely driven by stream flow effects on prey transport and competition for food resources with conspecifics, processes which are not incorporated by most laboratory-derived flow-foraging relationships (Naman et al., 2016; Piccolo et al., 2014). Declines in consumption at the lowest flows may be explained by reduced prey availability and increased conspecific fish density resulting in density-dependent foraging interactions (Grossman & Simon, 2020; Rosenfeld, 2017). Prey availability is known to decline substantially during severe low-water periods (Danehy et al., 2017; Suren & Jowett, 2006). Stream-dwelling salmonids may also concentrate within shrinking pool refuge habitats under these conditions, strengthening dominance hierarchies and intensifying competition for food resources (Ebersole et al., 2009; Rosenfeld et al., 2005; Sotiropoulos et al., 2006). In contrast, increased consumption towards the flow maximum likely results from enhanced prey availability associated with streambed scouring and inundation of gravel bars and riparian zones (Gibbins et al., 2007; Theodoropoulos et al., 2017). Moreover, numerous ephemeral channels drain hillslopes during high-water events, which likely contribute large fluxes of terrestrial prey to fish-bearing habitats (Wipfli et al., 2007). At high flows, these mechanisms expand the 'resource-shed' supporting drift-feeding fishes by transporting prey resources from a greater diversity of habitat types across a wider spatial extent (Power & Rainey, 2000). Other mechanisms, such as flow-induced foraging behaviour shifts known to occur in other salmonids, might explain increased consumption of larval and early-life-stage salmon seen in Dolly Varden under high-flow conditions (Figure 3; Bell et al., 2017; Fausch, 2014; Rossi et al., 2021). While not measured in this study, patterns of fish movement may also contribute to species differences in observed foraging patterns. Dolly Varden are known to move frequently and extensively throughout freshwater stream networks in southeast Alaska (Bryant et al., 2009). In comparison, juvenile Coho Salmon rearing in small freshwater streams display greater site fidelity and finer spatial-scale movement patterns (Armstrong et al., 2010; Weybright & Giannico, 2018). If fish move to exploit temporal variation of food resources in relation to streamflow, these behavioural attributes may contribute to observed foraging differences between species (Rossi et al., 2021).

While hydrologic conditions prior to salmon spawning were clearly influential on early-season fish foraging patterns, later pulse subsidy resources appeared more important in terms of cumulative annual consumption based on initial GAM outputs (Supporting Information). Modelled early-season flow-foraging relationships broke down with the arrival of the pulsed subsidy. Predicted consumption increased significantly after salmon spawning began and remained elevated regardless of flow (Figure 3) as fishes switched to consuming salmon eggs (Figure 2). This trend is consistent with saturating growth responses of freshwater fish during pulsed subsidy events, where consumption rates and growth primarily track spawning salmon density (Bentley et al., 2012). Moreover, our findings likely underrepresent the relative contribution of pulse subsidy resources to growth, given that salmon eggs can be up to three times as energy dense as invertebrate prey (Armstrong et al., 2010), which was not reflected in ash-free dry mass consumption values. Thus, a large majority of energy intake throughout the 2021 growing season was likely acquired from marine resources derived from the Pink Salmon pulse subsidy.

Although juvenile salmonids heavily exploited salmon-derived resources, this does not mean that salmon pulse subsidies are always more important than local environmental conditions to juvenile salmonid growth. Coho Salmon smaller than approximately 70 mm in total length experience gape limitation that can inhibit access to highly profitable salmon eggs during pulsed subsidy events (Armstrong et al., 2010). Gape-limited individuals may not benefit from pulse subsidies and could instead remain dependent on less energy-dense invertebrate prey for their entire freshwater life stage. Bioenergetic simulations incorporating interannual hydrologic variation at our study site revealed sizeable disparity in Coho Salmon growth trajectories among years, positing the hypothesis that antecedent hydrologic conditions are capable of controlling consumer access to salmon pulse subsidies. In higher water years, simulated age-1 Coho body size far exceeded the gape limit for egg consumption. In contrast, the two lowest water years (2018 and 2019) produced body sizes smaller than the gape limit required to consume salmon eggs by the onset of Pink Salmon spawning (Figure 4c). Thus, Coho Salmon in high-water years may be better suited to consume salmon eggs upon Pink Salmon arrival, whereas fish in low-water years may not. In a pulse subsidy exclusion scenario, end-of-July body-size disparity for Coho Salmon during low- relative to high-water years would likely be amplified in end-of-year body size due to continued dependence on local prey and environmental conditions. Such growth differences among years may have implications for annual patterns of system productivity and overwinter and marine smolt survival (Quinn & Peterson, 1996; Weitkamp et al., 2011).

While our simulations indicate that flow-induced growth trajectory shifts may occur, aspects of these findings may not reflect realistic ecological outcomes. For instance, flow-foraging relationships used to parameterize the bioenergetic simulation were restricted to the range of flows observed during a single study year (2021) and could mask important ecological thresholds that exist at flows beyond what we measured (Power et al., 2015; Rosenfeld, 2017). Our limited temporal scope of observation might also present issues with the accuracy of bioenergetic simulation predictions if variables such as starting fish body size, prey availability or stream thermal conditions were substantially different in other years (Deslauriers

et al., 2017). Lastly, it is possible that the poor growth outcomes predicted for 2018 and 2019 would not occur. Instead, we might expect fish to track more optimal environmental conditions and move out of the study reach to seek refuge habitats where conditions are more favourable for growth (Armstrong et al., 2010; Davey & Kelly, 2007; Freeman et al., 2022). Alternatively, fish may experience mortality from becoming stranded in disconnected aquatic habitats, or be unable to sustain basic metabolic processes (Davey & Kelly, 2007; Nagrodski et al., 2012). Nonetheless, we believe that general patterns observed in our simulation results are reasonable, as empirical studies have documented similar effects of streamflow on Coho productivity, albeit without a concrete mechanistic basis of explanation (Ebersole et al., 2009). To better validate these predictions, future research is necessary over a wider range of flow and longer time period than what we observed.

Hydrologic regimes throughout the coastal GOA are anticipated to experience more extreme high- and low-flow events in future (Musselman et al., 2018; Sergeant et al., 2020), requiring more nuanced explorations into possible synergistic effects between salmon pulse subsidies and antecedent hydrologic conditions on growth outcomes for juvenile salmon. At present, the coastal GOA region is a hydrologically diverse landscape of watersheds fed by glaciers, seasonal snowpack and year-round rain (Sergeant et al., 2020). However, as glaciers recede and precipitation shifts from snow to rain, hydrologic regimes will become more similar throughout watersheds across this landscape (Bellmore et al., 2022). At the same time, streams will become more prone to extreme flow conditions (Musselman et al., 2018; Sergeant et al., 2020). Previous modelling efforts suggest that shifting flow regimes can influence salmon populations via multiple mechanisms (Bellmore et al., 2023). Our study suggests that increased hydrologic variation and extreme flow event frequency associated with shifting flow regimes could intensify year-to-year Coho Salmon variation by mediating access to salmon egg pulse subsidies. Furthermore, shifting flow conditions are likely to alter the timing and magnitude of salmon spawning subsidies. Extreme conditions including redd-scouring winter floods (Sloat et al., 2017), lethal low flows during salmon spawning (Sergeant et al., 2017) and spatially shifting habitat suitability (Sergeant et al., 2020) may alter the nature of future salmon pulse subsidies, producing unexpected changes in juvenile salmonid growth conditions. Given that this region supports one of the largest Coho Salmon populations in the world, it is crucial to understand how local environmental conditions influence the capacity for watersheds to support juvenile salmon.

In summary, our research documented species-specific flow-foraging relationships for two stream salmonids prior to the arrival of a Pink Salmon pulse subsidy and elevated flow-independent rates of consumption after. Bioenergetic simulations revealed that real-world patterns of interannual hydrologic variation may shift early-season Coho Salmon growth trajectories, where higher water years generally improve growth relative to lower water years. This highlights the potential for antecedent local environmental conditions and a salmon pulse subsidy to interact with stream fish foraging and growth such that early-season hydrologic conditions might mediate exclusion or access to later-season salmon-derived resources, producing contrasting growth trajectory outcomes. This is important to consider in the context of regional climatic change, which is expected to bring increasingly stochastic flow regimes throughout the GOA landscape, with possible disruptions to important pulse subsidy-consumer dynamics. More broadly, this research shows that local environmental conditions are important to consider to better understand how ephemeral resource pulses shape patterns of consumer resource acquisition.

AUTHOR CONTRIBUTIONS

Kevin A. Fitzgerald, J. Ryan Bellmore, Jason B. Fellman and Jeffrey A. Falke conceived the ideas and devised the methodology of this study. Kevin A. Fitzgerald, Claire E. Delbecq and Matthew L. H. Cheng collected all field data. Kevin A. Fitzgerald, Matthew L. H. Cheng and J. Ryan Bellmore completed analyses. Kevin A. Fitzgerald led the writing of this manuscript, with contributions from J. Ryan Bellmore, Jason B. Fellman and Jeffrey A. Falke in all phases. All co-authors provided critical feedback and expertise to various drafts of this manuscript and have provided their final approval for its submission and publication.

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CONFLICT OF INTEREST STATEMENT

No authors have declared any conflicts of interest for this work.

DATA AVAILABILITY STATEMENT

The datasets and R scripts used in this study are original and will be available on the US Geologic Survey digital repository ScienceBase at https://doi.org/10.5066/P9EEEDB1 (Fitzgerald et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Two-panel table containing sample model ranks, *y*-intercepts, *p*-values associated with explanatory variables, AIC

scores, and model deviance explained across three possible models each before (a) and after (b) Pink Salmon spawning began.

Figure S1. Scatterplot of total lengths (*x*-axis) with age-class assignments for Coho Salmon captures plotted through time (*y*-axis). Individual points represent individual fish, with age class assignment specified by color (figure legend) and shape (square = age-2, triangle = age-1, circle = age-0). Black dotted line indicates the 70-mm gape-limit threshold, and the black dashed line separates the before pink salmon spawning time period (left) from after (right).

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