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Foraging modes and movements of *Oncorhynchus mykiss* as flow and invertebrate drift recede in a California stream

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Abstract: Salmonids frequently adapt their feeding and movement strategies to cope with seasonally fluctuating stream environments. *Oncorhynchus mykiss* tend to drift-forage in higher velocity habitat than other salmonids, yet their presence in streams with seasonally low velocity and drift suggests behavioral flexibility. We combined 3D videogrammetry with measurements of invertebrate drift and stream hydraulics to investigate the drivers of *O. mykiss* foraging mode and movement during the seasonal recession in a California stream. From May to July (2016), foraging movement rate increased as prey concentration and velocity declined; however, movement decreased in August as pools became low and still. In May, 80% of *O. mykiss* were drift-foraging, while by July, over 70% used search or benthic-foraging modes. Velocity and riffle crest depth were significant predictors of foraging mode, while drift concentration was a poor univariate predictor. However, top-ranked additive models included both hydraulic variables and drift concentration. A drift-foraging bioenergetic model was a poor predictor of foraging mode. We suggest that infall and benthic prey, as well as risk aversion, may influence late-summer foraging decisions.

Résumé : Les salmonidés adaptent fréquemment leurs stratégies d'alimentation et de déplacement selon les fluctuations saisonnières des milieux des cours d'eau. Si les *Oncorhynchus mykiss* ont tendance à s'alimenter d'organismes à la dérive dans des habitats de plus grande vitesse d'écoulement que d'autres salmonidés, leur présence dans des cours d'eau qui, en certaines saisons, présentent de faibles vitesses d'écoulement et de faibles concentrations de la dérive indiquerait une certaine souplesse comportementale. Nous avons combiné la vidéogrammétrie en 3D à des mesures de la dérive d'invertébrés et de l'hydraulique du cours d'eau pour étudier les facteurs qui modulent le mode de quête de nourriture et les déplacements des *O. mykiss* durant la récession saisonnière d'un cours d'eau californien. De mai à juillet (2016), la fréquence des déplacements de quête de nourriture augmentait à mesure que la concentration de proies et la vitesse du courant diminuaient; les déplacements ont toutefois faibli en août, alors que l'eau dans les fosses était devenue basse et stagnante. En mai, 80 % des *O. mykiss* s'alimentaient de la dérive, alors qu'en juillet, plus de 70 % utilisaient des modes de recherche ou d'approvisionnement benthique. La vitesse d'écoulement et la profondeur des crêtes de seuil étaient des indicateurs significatifs du mode d'approvisionnement, alors que la concentration de la dérive était un piètre indicateur univarié. Les modèles additifs les plus performants intègrent toutefois des variables hydrauliques et la concentration de la dérive. Un modèle bioénergétique de consommation d'organismes à la dérive ne prédit pas bien le mode d'approvisionnement. Nous proposons que les proies qui tombent dans le cours d'eau et les proies benthiques, ainsi que l'aversion pour le risque, pourraient influencer les décisions d'approvisionnement à la fin de l'été. [Traduit par la Rédaction]

Introduction

Substantial work has examined the fitness consequences of foraging behavior for juvenile salmonids. Much has focused on the energetics and position choices of drift-foraging, where fish hold at stations in the water column and make short forays into faster flows to intercept drifting invertebrate prey (Jenkins 1969; Fausch 1984; Hughes and Dill 1990; Nakano et al. 1999*a*). However, juvenile salmonids also forage in other, less studied ways (Harvey and Railsback 2014; Nielsen 1992; Nakano et al. 1999*a*). Search- or cruise-foraging salmonids actively move throughout the foraging patch, locating and attacking prey, without maintaining a focal point or even a specific directionality (Tippets and Moyle 1978; Puckett and Dill 1985; Nielsen 1992; Fausch et al. 1997; Harvey and Railsback 2014). A foraging mode distinction can also be made between search-foragers who focus their efforts on drift in the water column versus benthic prey on the stream bed (Nakano et al. 1999*a*).

Although the foraging mode of juvenile salmonids has long been a subject of research interest (Kalleberg 1958), few studies have investigated the drivers or ecological contexts that precipitate different foraging modes (Tunney and Steingrímsson 2012). In char (Fausch et al. 1997) and Atlantic salmon (*Salmo salar*) (Nislow et al. 1998), experimental reduction of drifting prey abundance caused a shift from drift-foraging to search- and benthic-foraging. Declining prey encounter rates have also been hypothesized to increase foraging movement in salmonids (Fausch and White 1981; Steingrímsson and Grant 2011). Foraging territory size tends to decline when food is abundant; however, a meta-analysis shows that the size of this effect is often small for stream-dwelling salmonids (Grant et al. 2017). In addition to food, velocity and velocity

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patterns drive habitat selection and swimming behavior (Fausch 1993; Liao 2007), influence capture probability and prey encounter rates (Naman et al. 2020*a*; Piccolo et al. 2008), and act as cues for foraging salmonids (Gowan 2007). These observations suggest that velocity and velocity patterns would also affect foraging mode decisions. Finally, water temperature affects foraging activity, as well as the metabolic costs and benefits of foraging (Sloat and Osterback 2013, Naman et al. 2020*b*). The dynamic phenology and spatial variability of drifting prey, flow velocity, and water temperature in many streams suggests that the interaction among these variables could drive seasonal and spatial changes in foraging mode for stream-dwelling salmonids.

Here, we quantify the foraging mode and movement of juvenile stream dwelling *Oncorhynchus mykiss* (resident "rainbow trout" or anadromous "steelhead") during the spring and summer streamflow recession of a small Californian stream. *Oncorhynchus mykiss* are considered to be primarily drift-foragers (Nakano et al. 1999*b*; Van Leeuwen et al. 2011; Rosenfeld et al. 2014), preferring habitats with higher velocities and more hydraulic complexity than other salmonids. Repeated studies have shown that *O. mykiss* tend to choose drift-foraging locations in high-velocity habitat where adjacent roughness elements afford holding stations with reduced swimming costs (Fausch 1993; Tucker and Rasmussen 1999; Van Leeuwen et al. 2011; Rosenfeld et al. 2014). However, the sustained presence of *O. mykiss* in the coastal Mediterranean climate streams of California (Shapovalov and Taft 1954) with very low or intermittent summer flow, when drift is minimal (Smith and Li 1982), requires more flexible foraging behavior. Harvey and Railsback (2014) and Caldwell et al. (2018) included a search-foraging mode in their energetic models for *O. mykiss* in Mediterranean streams; however, reported observations of search- or benthic-foraging in lotic *O. mykiss* are rare in the literature (but see Tippets and Moyle 1978 and Merz 2002). Given the importance of flexible foraging behavior for understanding salmon ecology and management (Dill 1983; Mittelbach et al. 2014; Nakano et al. 1999*a*), and the comparative lack of research on juvenile *O. mykiss* foraging in Mediterranean streams, a clearer understanding of seasonal changes in *O. mykiss* foraging behavior during the critical streamflow recession period is needed.

The spring and summer streamflow recession is an ecologically significant event in rain-fed streams with Mediterranean seasonality (Yarnell et al. 2015; Dralle et al. 2017). During the recession, streamflow declines following power laws (Dralle et al. 2017), and opportunities for foraging, movement, and growth of salmonids change rapidly (Hayes et al. 2008). In addition, as days lengthen in spring, water temperature and secondary (invertebrate) productivity increase (Gasith and Resh 1999; Bonada and Resh 2013), elevating both prey abundance and metabolic requirements for consumers like juvenile salmonids. Later in summer, drifting prey flux and concentration are expected to decline with velocity (Smith and Li 1982; Naman et al. 2016). These changing hydraulic and biotic conditions of the seasonal streamflow recession provide a natural experiment for investigating the seasonality and drivers of *O. mykiss* foraging behavior and movement.

We hypothesized that decreasing water velocity and drifting prey concentration would (*i*) lead *O. mykiss* to increase their foraging movement rates to maintain prey encounter rates, which would (*ii*) increase the proportion of search-foraging fish relative to drift-foragers. We further hypothesized that (*iii*) a seasonal decline in the energetic profitability of drift-foraging (the net rate of energy intake (NREI), modeled mechanistically from relationships between hydraulics and drifting prey; Hughes and Dill 1990) would predict timing of shifts from drift-foraging to search-foraging better than either hydraulic variables (e.g., depth, velocity) or drift concentration alone.

Methods

This study was conducted in Elder Creek, a 16.7 km^2 tributary of the upper South Fork Eel River in Northern California (39.7181°N, 123.6527°W). We studied the first 4 km of Elder Creek above its confluence with the South Fork Eel River. The stream has a coarse bed dominated by cobbles and boulders. Gradients range from 2% to 5% in riffles, averaging 2.4% over the 4 km whole study reach (McBain and Trush and Trout Unlimited 2000). The South Fork Eel River basin, including Elder Creek, has a Mediterranean climate, with >90% of the annual rainfall occurring from November through April (Mierau et al. 2018). Elder Creek experiences the characteristic Mediterranean flow recession between April and October (Dralle et al. 2017), with typical summer low flows from 0.015 to 0.03 $m^3 \cdot s^{-1}$ and rarely dropping below that range. Unlike many small Mediterranean streams, Elder Creek maintains perennial flow over much of its course, even during multiyear drought (Lovill et al. 2018). The perennial flow of this small basin in an otherwise Mediterranean climate is supported by the thick critical zone, of its watershed, which is underlain by thick water-holding argillite shales in the Northern California coastal belt (Rempe and Dietrich 2018; Lovill et al. 2018). Perennial flow in Elder Creek supports continuous (although seasonally varying) production and drift of benthic invertebrates.

Site-selection and hydraulic measurements

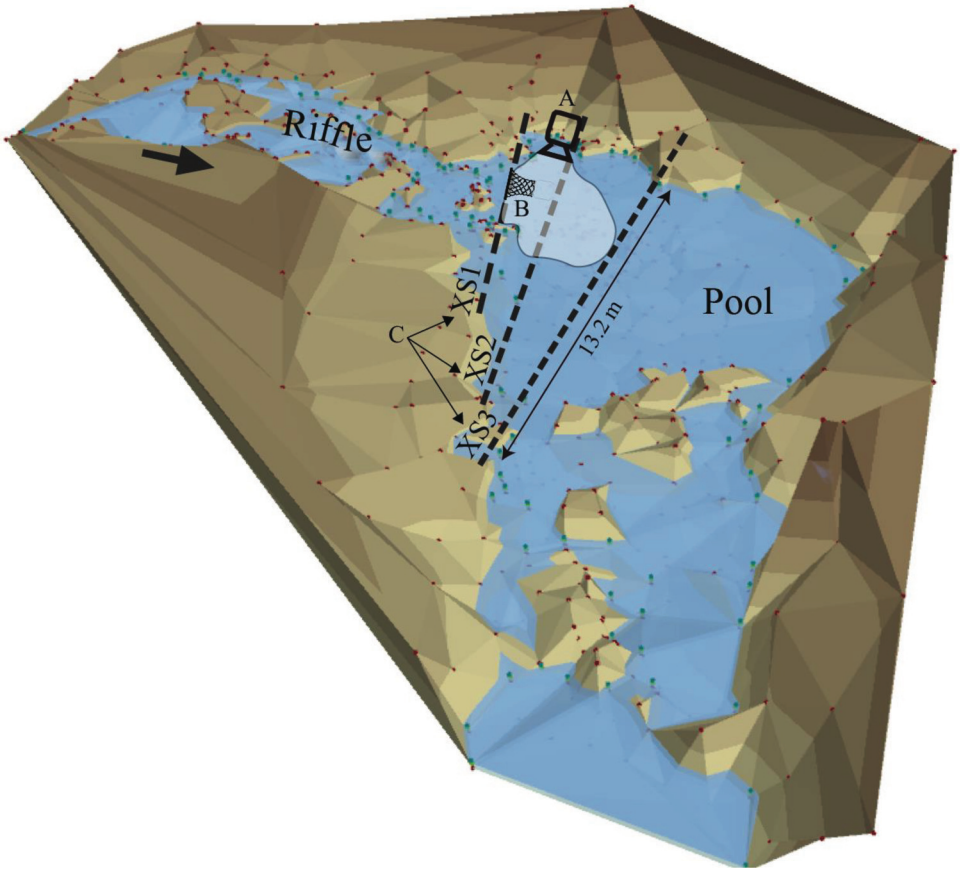
Habitat units (riffle–pool sequences) were selected for study based on two primary criteria: (*i*) the site was a riffle–pool sequence that supported multiple age classes of foraging *O. mykiss*, and (*ii*) the site had suitable morphology for filming videos, which were shot perpendicular to flow. Thirty sites meeting these two criteria were identified within our study reach, and seven were selected, based on their favorability for filming and the total number of sites we could physically sample in a day. To evaluate the relationship between invertebrate drift and foraging behavior, we focused video recording on the head of each pool (hereinafter pool head patch), where fish were most likely to intercept drifting invertebrates during the summer low flow period (Smith and Li 1982; Harvey et al. 2006; Van Leeuwen et al. 2011).

Sampling began on 18 May 2016 and ended on 16 August 2016. Fish behavior, invertebrate drift, and hydraulic measurements were taken on 26 and 27 May, between 18 and 20 June, between 5 and 6 July, between 26 and 27 July, and between 15 and 16 August. Streamflows in Elder Creek declined during the study period from 0.15 $m^3 \cdot s^{-1}$ on 18 May to 0.02 $m^3 \cdot s^{-1}$ on 17 August 2016 (refer to online Supplementary Material, Fig. S1[1]). Streamflow and water temperature were retrieved from USGS gaging station 11475560 "Elder Creek near Branscomb CA", which is 0.6 km upstream from the Elder Creek's confluence with the South Fork Eel River. Water temperature ranged from 9.8 °C on 23 May to 19.8 °C on 29 July.

At each study site, three cross-stream transects were established in the pool head patch — one where invertebrate drift enters the pool from the riffle upstream, a second bisecting the focal area for video analysis, and a third over the maximum depth of the pool — which marked the downstream boundary of our designated "pool head patch" (Fig. 1; Table 1). Depth and velocity were measured at 0.5-m increments along each cross-section. Velocity was measured at 0.6 of depth, an estimate of average water column velocity (Rantz 1982), with a SonTek Flow Tracker (ADV series) acoustic doppler velocity profiler. Volume was calculated between each cross-section on each survey date, using the average end method (Taube 2000). Depth of flow was also measured where the thalweg bisects the downstream riffle crest of each pool at the "riffle crest thalweg (RCT)" (Hilton and Lisle 1993; Mierau et al. 2018). The hydraulic relationship between this riffle crest depth and streamflow is sensitive to

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0398.

Fig. 1. A topographic map of a riffle–pool unit in Elder Creek. The map was created by converting surveyed elevation data into a triangulated irregular network dataset using ArcMap 10.3. The map shows (A) the video pin location where the cameras were anchored, (B) the invertebrate drift net location, and (C) transects (XS) where depth and velocity where measured. The light blue patch represents the approximate area that was filmed. The area between XS1 and XS3 is the "pool head patch". The red dots are topographic survey points, and the green dots represent the surveyed water surface at 0.15 $m^3 \cdot s^{-1}$.



channel morphology (Emery et al. 2003) and has been shown to be primary control of upstream pool depth and velocities (Lisle 1987; Pasternack et al. 2008). Since fish respond to complex 3D flow patterns (Liao 2007), which were impractical to measure empirically in the field, we used RCT depth and maximum pool velocity as a proxies for seasonal change in pool hydraulics (Pasternack et al. 2008; Chiu and Tung 2002).

Analysis of fish behavior

Videos of fish behavior were collected with stereo-pairs of mounted GoPro cameras (model: HERO 4 Black, recorded at 30 frames per second with 1080p resolution) installed at monumented stations in each pool (Fig. 2, Supplementary Fig. S2[1]). Recordings lasted ~30 min and were collected between 4 pm and 6 pm every evening during each of five survey events. We selected this crepuscular period to monitor fish behavior because it is associated with increased foraging activity for *O. mykiss* (Railsback et al. 2021) and increased behavioral drift of invertebrate prey (Svendsen et al. 2004). Video of fish behavior in the pool head patch was used for scan samples of foraging mode over short, fixed time intervals (Altmann 1974) and to track the foraging movement rate of individuals through time and space (Neuswanger et al. 2016).

Video analysis of foraging mode

Video scan samples were used to quantify the number and proportion of *O. mykiss* foraging modes in each video. Foraging mode and behavioral events were defined based on common literature descriptions (Table 2). We allowed at least 3 min after the camera was placed in the pool for fish to resume their normal behavior. This interval was determined after watching multiple videos and measuring how long it took fish to resume a consistent foraging behavior after cameras were installed. A foraging mode was assigned to every fish observed in each scan. Occasionally (and rarely) juvenile fish were determined to be sheltering or not foraging in any evident way (Supplementary Table S1[1]). To determine a fish's foraging mode, a reviewer watched the animal in motion for a 10s video interval. We qualitatively determined 10 s as an adequate time to discern foraging mode, but a short enough interval that fish behavior and density to were not expected to change. We used a constant sampling interval in which reviewers watched the first 10 s interval for every 30 s of video, counting the number of animals that were engaged in specific foraging modes during the scan. Other behavioral events, such as surface strikes, attacks, or nips, (Table 2), were also counted and summed within each scan. Two of the seven study pools were unsuitable for video scans due to poor lighting conditions. From the remaining five sites, we analyzed one video per date (five dates) and site (five sites) for a total of 25 videos. The number of scan samples was constrained by light and turbidity. If visibility was impaired, we skipped that 10 s interval. The minimum number of scans per video was 15 and the maximum number was 26.

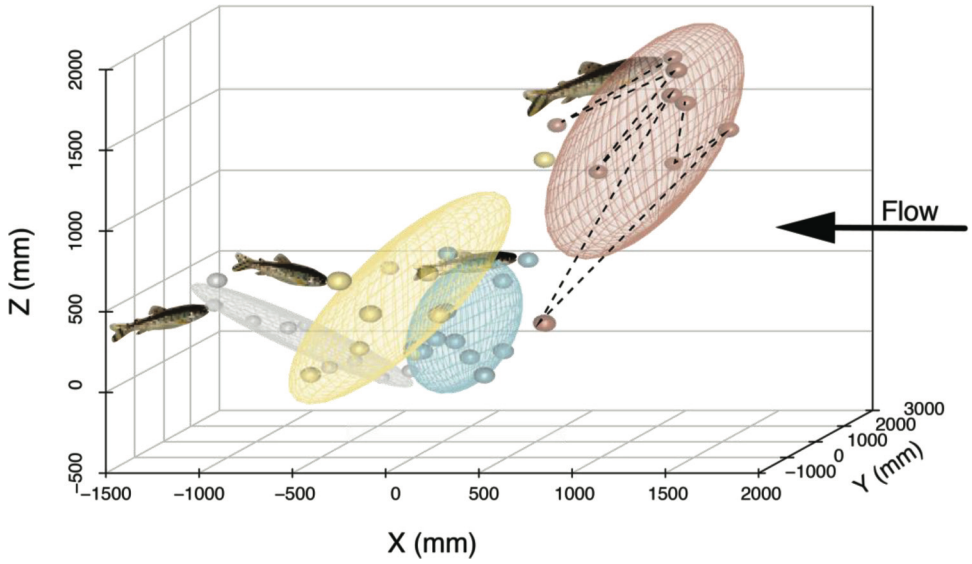
The maximum number of *O. mykiss* observed in any 10 s scan was used to estimate pool head patch abundance. Pool head patch density was estimated by dividing fish abundance by the

Table 1. Operational definitions for habitat, hydraulic, invertebrate, and fish variables.

Terms and variables	Operational definition	Unit
Pool head patch	The head of the pool — from where the upstream riffle enters the pool to the maximum pool depth (Fig. 1)	m^3
Whole pool	The entire pool from where the upstream riffle enters the pool to the downstream riffle crest	m^3
Drift $flux_{Numbers}$	No. of invertebrates caught, per hour, in thalweg drift net	$no.\cdot h^{-1}$
Drift $flux_{Mass}$	Mass of invertebrates caught, per hour, in thalweg drift net	$mg\cdot h^{-1}$
Drift $concentration_{Numbers}$	No. of invertebrates per volume	$no.\cdot m^{-3}$
Drift $concentration_{Mass}$	Mass of invertebrates per volume	$mg\cdot m^{-3}$
Q	Streamflow	$m^3\cdot s^{-1}$
Temp	Water temperature	°C
Max depth XS_*i*	The maximum depth measured on cross-section *i*	m
Max depth	Maximum depth at XS3 (e.g., max. pool depth)	m
Max velocity XS_*i*	The maximum velocity measured on section *i*	$m\cdot s^{-1}$
Avg velocity XS_*i*	The average velocity measured on section *i*	$m\cdot s^{-1}$
RCT_*i*	Riffle crest depth measurement taken at downstream hydraulic control	cm
Foraging movement rate	The distance that foraging *O. mykiss* (within the pool head patch) traveled per unit time (e.g., microhabitat movement)	$mm\cdot s^{-1}$
Pool head patch counts	The number of *O. mykiss* observed in video scans at the head of the pool	Individuals
Whole pool counts	The number of *O. mykiss* observed during whole pool snorkel counts	Individuals
Pool head patch density	Count of *O. mykiss* observed in video scans at the head of the pool, divided by pool head patch volume	$no.\cdot m^{-3}$

Note: Bold font denotes predictor variables used in statistical analysis.

Fig. 2. A schematic of 3D fish location data from VidSync for four *O. mykiss* in an Elder Creek pool during 30 s of a VidSync survey. For each *X*, *Y*, *Z*, location (shown as spheres), a fish ID, timestamp, and qualitative behavior are defined. An example of foraging movement path (30 s) for foraging movement rate analysis is shown with the dashed line as the dominant fish (red) engages in a foray–return pattern of drift-foraging. For illustrative purposes, best-fit ellipses are fit over 3D occupied volumes using the R package gl.



volume of the pool head patch (defined as the volume between XS1 and XS3 in Fig. 1). In addition to video, each pool was snorkeled three times during the summer (26 May, 21 June, and 17 August) to compare trends in pool head patch abundance and density with estimated abundance and density of *O. mykiss* in the whole pool. The snorkeler entered below the downstream riffle crest of each pool and moved upstream slowly and carefully, face forward. Given the small size of most study pools, much of the pool volume could frequently be observed from the downstream riffle crest. Fish were only counted once they were downstream of the observer to minimized double counting. All salmonids observed during snorkel surveys were identified to species and binned in one of five size classes to estimate age: ≤30 mm ~ fry, 30 to 80 mm ~ young of year, 80 to 120 mm ~ 1 year old; 120 to 200 mm ~ 2+ years old (Supplementary Table S2[1]).

VidSync analysis for foraging movement rate

In addition to scan samples, individual *O. mykiss* were tracked on the pool head patch video using the open source software VidSync (Neuswanger et al. 2016). Fish tracking was used to compute the foraging movement rate ($mm\cdot s^{-1}$) within the pool head patch in (Table 1). VidSync allows the user to triangulate a 3D position in relative space, using known lines of sight from two or more cameras. We followed the video correction and calibration procedure described in Neuswanger et al. (2016). The primary output data from the Vidsync analysis were 3D positions and timestamp of each location observation (Fig. 2). These data were organized by a fish ID (a unique ID assigned to each tracked fish observation) and sampling event (Fig. 2). Videos from the other three of our seven study pools were unsuitable for VidSync analysis because camera placement on two or more dates did not

Table 2. Definition of foraging behaviors used in video scan samples.

Behavior	Definition
Foraging mode	
Drift-foraging	Fish holds focal points in the water column and makes short forays to intercept drift, with only occasional attacks on benthic prey near their focal points (Nakano et al. 1999*a*).
Benthic-foraging	Fish primarily cruise over larger areas of stream bed and capture benthic prey by making forceful attacks at the substrate (Nakano et al. 1999*a*).
Search-foraging	Fish undertake continuous undirected swimming, foraging was not associated with a focal point, and fish consumed drift, falling, or benthic prey (adapted from Nielsen 1992).
Behavioral event	
Surface strike	A fish swims towards the surface and either attempts to or successfully bites an item floating on or just under the water surface (Suttle et al. 2004).
Attacks	A fish makes a rapid, aggressive darting approach toward another fish without making direct contact ("attacks" in Nielsen 1992).
Nips	A fish rapidly approached another fish and gives it a bite (Nielsen 1992).

provide adequate overlapping views that encompassed the focal foraging areas in each pool. From the remaining four sites, we analyzed one video per date (five dates) and site (four sites) for a total of 20 videos.

Since fish tracking is time intensive, we subsampled each video for VidSync analyses. Within each video we selected the 3 min clip with the highest counts of *O. mykiss*. Within this 3 min clip, we tracked the nose-point location of each observed *O. mykiss* over repeated 3 s intervals until 3 min expired or the fish left the video frame. The maximum number of location data points for a focal individual was therefore $n = 60$ (180 seconds / 3 seconds per data point), although most fish were tracked for fewer than 60 locations because fish would leave the field of view. In addition, to test the accuracy of length estimates from VidSync, we measured the length of a known object within our field of view five times for each video. Errors ranged from >1% to 6%, which are higher than reported by Neuswanger et al. (2016), but still achieve a level of precision much greater than snorkeling or bankside estimates.

Invertebrate drift

Immediately after our video filming was completed, drift was sampled for 2 h (±10 min) between 5 pm and 7 pm, when diel peak drift of common invertebrates (especially baetids and chironomids) has been reported (Waters 1972; Statzner and Mogel 1985; Schreiber 1995 cited in Svendsen et al. 2004). Invertebrate drift was collected at each of the seven study pools during each of the five primary sampling events between May and August 2016. Thirty-five samples of drift were collected (one at each of seven sites on each of five sampling events) using a circular drift net (30 cm diameter mouth aperture, 500 μm mesh). The drift net was installed just below the water surface along the most upstream cross-section at the head of the pool (Fig. 1); cross-stream position of the net was adjusted on each occasion to capture the region of highest velocity at each sampled streamflow. Drift samples were elutriated through 500 μm mesh and preserved in 100% ethanol. In the laboratory, drift samples were sorted and invertebrates identified to family or genus (Merritt et al. 2008) under 10× magnification. Samples were also categorized as being aquatic or terrestrial in origin. Each invertebrate was measured to the nearest 0.5 mm under a dissecting scope and biomass (mg dry mass) was estimated from published length to dry mass relationships (Benke et al. 1999; Sabo et al. 2002). Drift flux ($mg \cdot h^{-1}$) was computed by summing the mass of drifting invertebrates captured in the drift net and dividing the total mass by the duration of the drift sample. Drift concentration ($mg \cdot m^{-3}$) was computed by dividing drift flux by the discharge through the drift net ($m^3 \cdot s^{-1}$).

Net rate of energy intake (NREI)

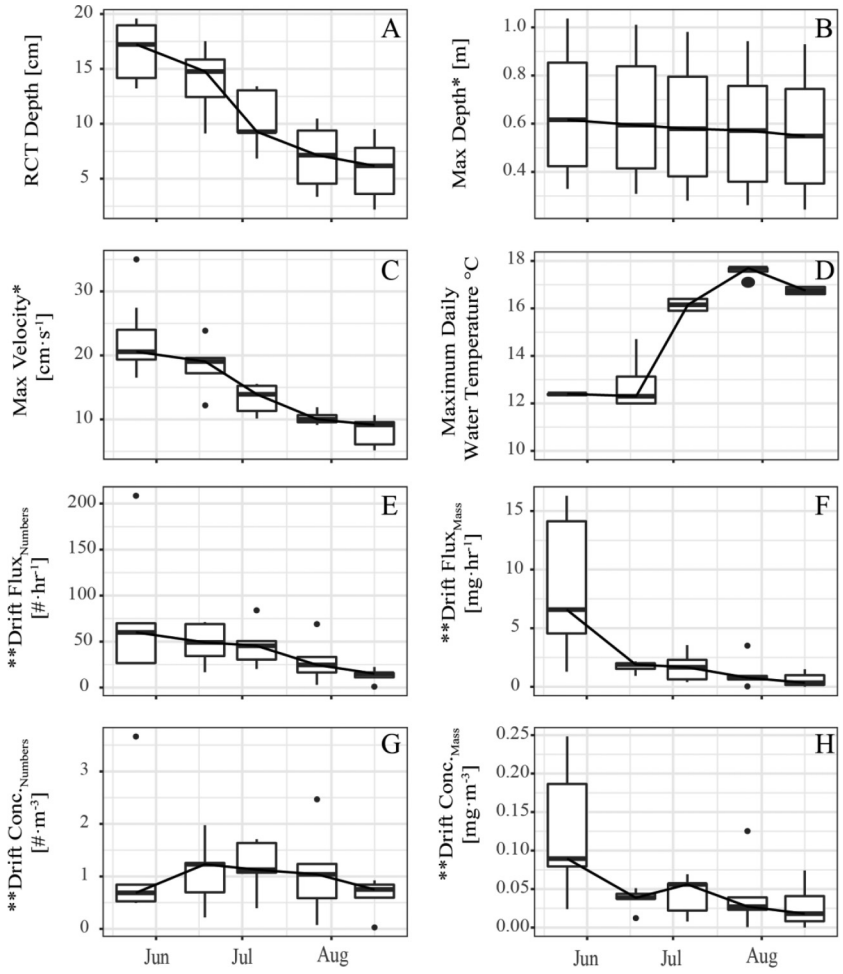
We estimated seasonal trends in drift-foraging profitability in the five video-study pools with a simplified drift-foraging bioenergetic model (Caldwell et al. 2018). The energetics equations for the model are based on Rosenfeld and Taylor (2009) and Hayes et al. (2000). The model uses drift concentration, discharge through the foraging volume, fish size, and prey size to quantify gross energetic intake rate — a product of capture probability, drift concentration, and discharge through foraging volume and energy expenditures based on swimming costs — a function of fish size and focal point velocity (Caldwell et al. 2018; Rosenfeld and Taylor 2009). Water temperature was incorporated into the swimming costs (following Rosenfeld and Taylor 2009); however, we assumed a constant energy assimilation efficiency of 0.6 (Tucker and Rasmussen 1999). Fish focal point velocity was estimated as the velocity (measured at 0.6 total depth) at the thalweg of cross-section 1 at the head of each pool (Fig. 1). The NREI ($J \cdot s^{-1}$) is the net energy acquired by juvenile fish for growth (gross energy intake – swimming and metabolic costs). The model was run for each date and site combination for which we had video and drift data in the summer of 2016, for a total of 25 model runs (five sites × five dates).

Since our intent was simply to track the phenology of drift-foraging profitability, rather than estimate size- and habitat-specific NREI, we modeled NREI for a single 100 mm drift-forager (approximately the mean size of *O. mykiss* observed in the pool head patch over the summer) at a single foraging location in the channel thalweg at the head of the pool. We chose to model this location to represent the most profitable drift-foraging position in the pool. We typically observed that this position was occupied by the dominant foraging fish. Many previous studies have shown the head of the pool to be preferred by drift-foraging *O. mykiss* (Harvey et al. 2006; Smith and Li 1982; Van Leeuwen et al. 2011). While we could have modeled NREI at multiple downstream locations, this would introduce uncertainty because of the need to scale drift concentration down from our measurement location (the head of the pool) to downstream and edgewater locations, accounting for new recruitment from benthos and losses from upstream consumption and settling of drift. Although these issues are surmountable with adequate sampling (e.g., following methods in Hayes et al. 2016), our intent was to determine how well drift-foraging NREI predicted the timing of behavioral shift to search-foraging and the head of the pool is where velocity and prey concentration are expected to be most dynamic (Harvey et al. 2006). In addition, Caldwell et al. (2018) noted that NREI for different size classes of drift-foragers and foraging locations downstream from the head of the pool locations followed a similar seasonal pattern over the hydrograph recession, although the magnitudes differed.

Statistical analysis

The drivers of *O. mykiss* foraging mode were evaluated using generalized linear mixed effects models in R version 3.5.1 (R Core 2017). Dependent variables were the relative proportions of foraging modes (drift, search, and benthic) across five pools and five sampled

Fig. 3. Seasonal trends (May and August 2016) in (A) riffle crest thalweg (RCT) depth, (B) maximum pool depth, (C) velocity, (D) water temperature, (E and F) invertebrate drift flux, and (G and H) invertebrate drift concentration (Drift Conc) for Elder Creek pools. Median values for each date are connected with straight lines, boxes show 25%–75% quartile range, and whiskers show ~95% confidence intervals.



* Measured in the pool head patch
** Entering thalweg drift net at the head of the pool (located on XS1)

dates. The movement of foraging fish followed a nonlinear pattern across the study period, so we chose to analyze movement with descriptive statistics rather than mixed effects models. We separated the predictor variables (Table 1) a priori into four categories: pool hydraulics variables, drifting prey variables, combined variables (prey + hydraulics), and NREI (which integrates hydraulics and prey mechanistically). We organized the models this way to provide heuristic value – since frequently stream ecologists and managers cannot measure or compute all of these variables.

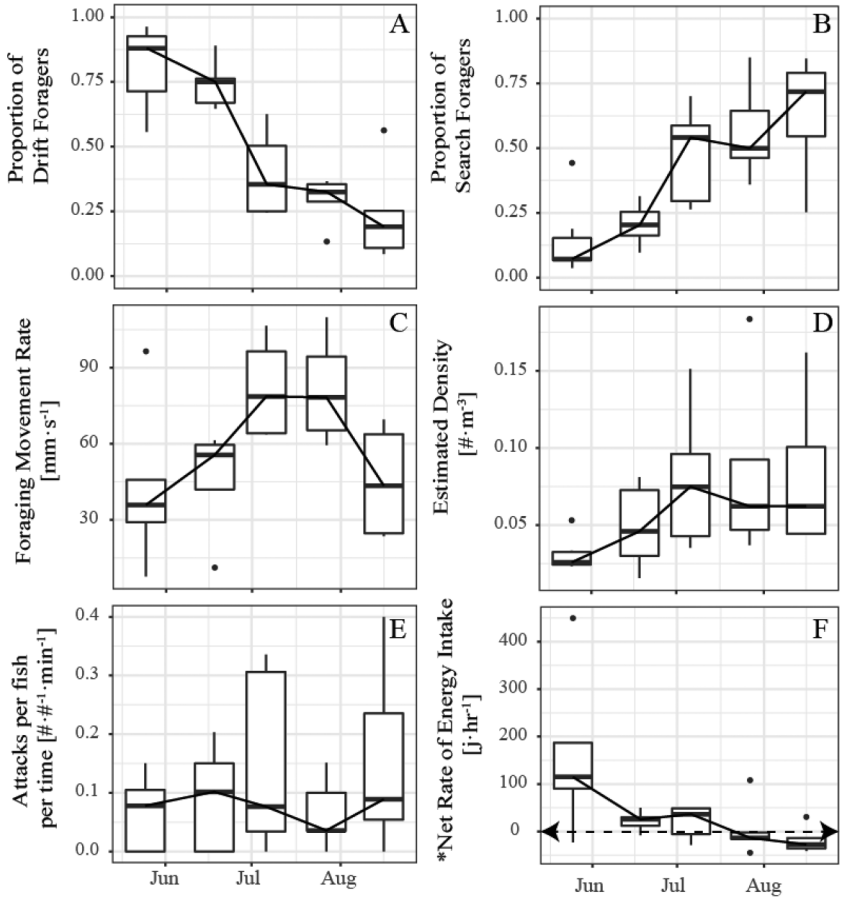
- **Pool hydraulics:** streamflow; velocity; RCT depth
- **Drifting prey**: drift concentration$_{Numbers}$; drift concentration$_{Mass}$
- **Hydraulics + prey:** all combinations of each noncolinear variable above
- **NREI**: computed net rate of energy intake for a 100 mm drift-foraging *O. mykiss*

Within each category, we built models by separating colinear terms (using an arbitrary threshold of 0.5 Pearson coefficient). This process resulted in 12 models for predicting each foraging mode — for a total of 36 models. We also controlled for fish density in the pool head patch and water temperature by including them as fixed effects in each model.

Because our dependent variables were proportions, we used generalized linear mixed effects models from the GLMM package in R (glmer command). A binomial distribution with logit link function was assigned, and weights were determined based on the total behavioral observations of each scan sample (Bolker et al. 2009). Our study used a crossed sampling design in which each pool was sampled on multiple dates, multiple pools were sampled on each date, and there was more than one observation per date–pool combination. Therefore, random effects were assigned for "study site", "date", and "date nested within site" (Bolker et al. 2009).

All models were ranked using Akaike information criterion modified for small sample sizes (AIC_c), to assign AIC weights (Wagenmakers et al. 2004), reflecting the probability that a given model was the most parsimonious model within our candidate model set (Burnham and Anderson 2004). In addition we evaluated the marginal r^2 (proportion of variance explained by the fixed effects) and conditional r^2 (proportion of variance explained by both fixed and random effects) values for a generalized linear mixed effects model, calculated using the r.squared GLMM function in the MuMIN package in R (Nakagawa and Schielzeth 2013). The results of these statistical models were evaluated against established theory of salmonid foraging behavior to interpret our findings.

Fig. 4. The seasonal phenology of (A and B) *O. mykiss* foraging mode, (C) foraging movement rate, (D) density, and (E) aggression in the pool head patch, as well as (F) computed net rate of energy intake for a 100 mm drift-foraging *O. mykiss* in each pool. Median values for each date are connected with straight lines, boxes show 25%–75% quartile range, and whiskers show ~95% confidence intervals.



*NREI computed for a 100mm, thalweg positioned, drift foraging O. mykiss
Dashed line represents zero NREI and growth potential.

Results

Seasonal trends in hydraulic habitat, food flux, and fish abundance in Elder Creek pools

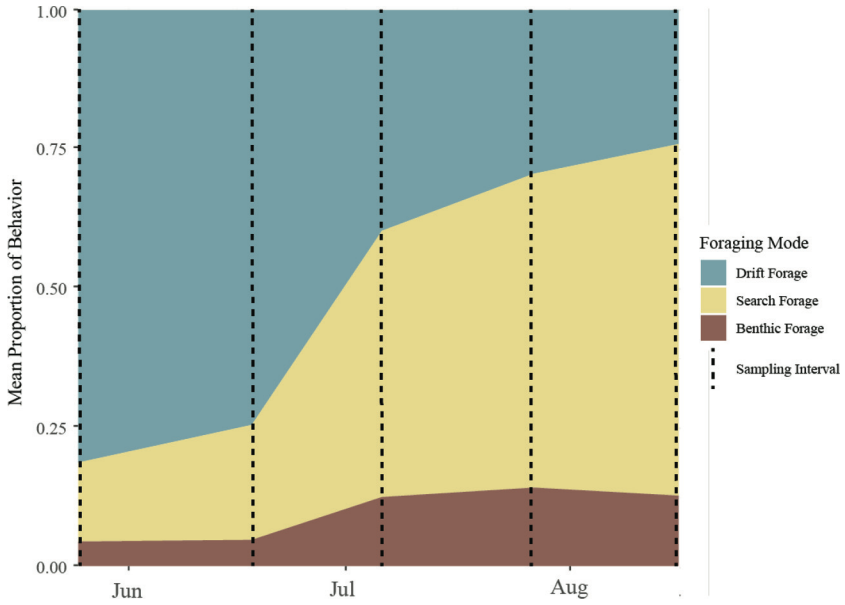
The hydraulic variables (pool maximum depth, velocity, RCT depth, and pool volume) all declined with streamflow in all pools between May and August (Fig. 3A–3D). Streamflow, RCT depth, and maximum velocity declined exponentially, but maximum pool depth (and volume) declined at a slow, nearly constant rate (Figs. 3A–3C). Water temperature was similar between May and June (mean of 12–14 °C) but increased rapidly to a mean of 17.4 °C in late July, before slightly decreasing to 16 °C in August. The average flux of individual drifting invertebrates (no.·h^{-1}) was highest in May and June, while average concentration of individual drifting invertebrates (no.·m^{-3}) peaked in early July at most sites (Figs. 3E and 3G). However, the flux and concentration of drifting invertebrate biomass (mg·h^{-1} and mg·m^{-3}, respectively) were highest in May by a wide margin (Figs. 3F and 3H). The average length of drifting invertebrates steadily declined from April to August, with the largest invertebrates drifting in May (Supplementary Fig. S3[1]). The rate of terrestrial invertebrates in the drift was highest in early July (Supplementary Fig. S4[1]), although drift is probably a poor representation of the seasonal infall of terrestrial invertebrates since many of them are consumed before they drift downstream. Although 120 unique taxa of drifting invertebrates were identified, four taxa — Simuliidae, Brachycentridae, Baetidae, and Chironomidae — made up 79% of the individual invertebrates in the drift. *Micrasema* (a small-cased brachycentrid caddisfly) alone made of 38% of all individuals counted.

Oncorhynchus mykiss counted during snorkeling observations in Elder Creek pools increased by almost an order of magnitude between May (26 fish observed in seven pools) and August (218 fish observed in seven pools; Supplementary Fig. S5[1]). Pool head patch densities doubled between May (mean density = 0.032 individuals·m^{-3}; pool head patch count = 4.6 individuals) and July (mean density = 0.082 individuals·m^{-3}; pool head patch count 9.8 individuals; Fig. 4D and Fig. S6[1]). After peaking in late July, pool head patch density declined slightly between late July and August (Fig. 4D). We saw almost no direct contact (nips) and so we reported only attacks (aggressive approach) in Fig. 4E. Although the range of attack incidents (between videos) increased in July and August when fish density was highest, the mean number of attacks per time remained similar between May and August (Fig. 4E). Pool head patch counts and pool-wide counts from the snorkel surveys followed similar trajectories, although counts increased faster over the summer in snorkel observations of the whole pool than in video scans of the pool head patch (Supplementary Fig. S6[1]).

Seasonal patterns of *O. mykiss* foraging movement

Oncorhynchus mykiss foraging movement rates were lowest in May (mean = 35 mm·s^{-1}) and steadily increased to a peak in late July (mean = 81 mm·s^{-1}), but later declined between late July and

Fig. 5. Seasonal patterns in the cumulative proportion of drift-, search-, and benthic-foraging *O. mykiss*, aggregated across five study pools in Elder Creek. The dashed vertical lines show the video sample dates (and correspond to the boxplot dates in Figs. 3 and 4).



August (mean = 45 mm·s^{-1}; Fig. 4C). Peak foraging movement was observed in early July in almost all sites. During the pre-peak movement period (May to early July), drift-foraging was the most common behavior of *O. mykiss* in all study pools. During this period, most observed fish apparently foraged within small focal volumes, moving short distances (typically 3–6 cm) to capture prey. Between May and early July, movement increased with fish density in the pool head patch and with decreasing pool velocity and RCT depth. Between early July and August, search-foraging was the dominant behavior, and fish tended to occupy larger volumes than they did in May. Peak foraging movement corresponded with the warmest observed temperatures, both of which occurred in July (Supplementary Fig. S7[1]). *Oncorhynchus mykiss* foraging movement, however, decreased by half between late July and August, as pools became low and still, and both hydraulic variables and drift concentration were near their late-summer nadir (Figs. 3G–3H).

Seasonal patterns of *O. mykiss* foraging mode in Elder Creek pools

We completed 654 scan samples from five pools, and recorded 3104 occurrences of various foraging behaviors (Supplementary Table S1[1]). Drift-foraging (49%) and search-foraging (39%) were most common, while attacks on the benthos accounted for only 12% (Figs. 4A–4B). Approximately 1% of observations were not associated with foraging or aggression (Supplementary Table S1[1]). Strong seasonal trends were observed in the proportion of drift-, search-, and benthic-foraging *O. mykiss* in Elder Creek pools from May to August in 2016 (Figs. 4A–4B and Fig. 5). In May, an average of 80% of *O. mykiss* in the pool head patch were drift-foraging. Drift-foraging decreased as search-foraging increased, with the proportion of search-foragers exceeding drift-foragers by mid-July. By August, 63% of observed *O. mykiss* were search-foraging and 13% of were benthic-foraging, which was equal to the proportion of drift-foragers in August (Fig. 5; Supplementary Table S1[1]).

In univariate models, hydraulic indicator variables were the strongest predictors of the proportion of fish that were drift- and search-foragers. Maximum velocity and riffle crest depth, independent of drift data, were significant positive predictors of the proportion of drift-foraging *O. mykiss* and significant negative predictors of the proportion of search-foraging *O. mykiss* (Table 3A and 3B). In univariate (prey only) models, drift concentration was a weak predictor of foraging mode. However, the top statistical models for predicting the proportion of drift- and search-foragers included both hydraulics and drift concentration, and both variables were significant for this combined model (Table 3A and 3B). Benthic-foraging was poorly predicted by any of the combined mixed effects models (Table 3C).

Discussion

The phenology and drivers of foraging movement rate

Between May and late July, foraging movement rate within the pool head patch (Table 1) increased as expected, while drift concentration and velocity both declined. However, we observed a decrease in foraging movement rate between late July and August during the lowest velocities and drift concentrations (Fig. 4C). Declining prey encounter rates are a driver of increasing movement in foraging animals (Holling 1959) and explicitly for salmonids (Fausch and White 1981; Steingrímsson and Grant 2011). However, the benefits of increased prey encounter rates (due to increased movement) are balanced against the risks and costs associated with increased movement. For example habitat contraction and reduced hydraulic cover (surface turbulence) at lower flows can increase predator avoidance behavior, which also reduces the foraging movement of salmonids (Dill 1983; Brown 1988; Harvey and White 2017; Naman et al. 2020*b*). We observed that surface turbulence, an important source of cover from avian and terrestrial predators (Allouche and Gaudin 2001), extended far into pools in May, but was absent from most pools by August, when fish were much more visible from above. We also noted that fish would take longer to return to normal foraging after we installed the cameras in August. Thus, our anecdotal observations suggest that predator avoidance and fear, in addition to declining profitability of foraging, may have reduced movement in late summer, as we observed between late July and August.

Behavioral theory and empirical observations show that increased metabolic demand at warmer water temperatures can also lead to reduced foraging and movement in salmonids (Smith and Li 1982; Nielsen 1992; Sloat and Osterback 2013). Thus, it might seem counterintuitive that we observed peak foraging movement rates and search-foraging behavior in late July (Fig. 4), which was also the sampling date with the warmest stream temperatures

Table 3. The results of generalized linear mixed effects models for predicting the proportion of (A) drift-, (B) search-, and (C) benthic-foraging *O. mykiss* across five sites.

A. Proportion of drift-foragers				
Ranked model(s)	Variables in ranked models	ΔAIC_c	AIC weights[a]	r^2 m/c[b]
Hydraulic + prey	**RCT_*i* + Drift concentration$_{Mass}$**	**0**	**0.95**	**0.30/0.34**
Hydraulic	RCT_*i*	5.8	0.05	0.28/0.34
Prey	Drift concentration$_{Numbers}$	15.5	0	0.25/0.40
NREI	NREI (J·h^{-1})	16.5	0	0.24/0.39
	Parameter	Coefficient	SE	Pr(>|*z*|)
Parameter coefficients in hydraulic + prey model	RCT_*i*	8.24	1.34	*7.00E-10*
	Drift concentration$_{Mass}$	10.82	3.16	*6.20E-04*
	Density in pool head patch	−0.09	0.17	0.6
	Maximum daily temperature	0.04	0.12	0.75
B. Proportion of search-foragers				
Ranked model(s)	Variables in ranked models	ΔAIC_c	AIC weights[a]	r^2 m/c[b]
Hydraulic + prey	**RCT_*i* + Drift concentration$_{Mass}$**	**0**	**0.91**	**0.27/0.34**
Hydraulic	Max velocity	4.7	0.08	0.28/0.37
Prey	Drift concentration$_{Mass}$	11.8	0	0.20/0.37
NREI	NREI (J·h^{-1})	13.7	0	0.18/0.36
	Parameter	Coefficient	SE	Pr(>|*z*|)
Parameter coefficients in hydraulic + prey model	RCT_*i*	−8.98	1.76	*3.29E-07*
	Drift concentration$_{Mass}$	−19.09	4.86	*8.55E-05*
	Density in pool head patch	0.20	0.15	0.16
	Maximum daily temperature	−0.19	0.14	0.19
C. Proportion of benthic-foragers				
Ranked model(s)	Variables in ranked models	ΔAIC_c	AIC weights[a]	r^2 m/c[b]
Hydraulic model	*Q*	0	0.3	0.10/0.26
Prey concentration	Drift concentration$_{Numbers}$	0.12	0.28	0.10/0.25
Drift-foraging NREI	NREI (J·h^{-1})	0.19	0.27	0.11/0.27
Hydraulic + prey	Max velocity + Drift concentration$_{Numbers}$	1.48	0.14	0.11/0.27
	Parameter	Coefficient	SE	Pr(>|*z*|)
Parameter coefficients in hydraulic model	*Q*	−0.138	0.241	0.568
	Density in pool head patch	0.125	0.215	0.561
	Maximum daily temperature	0.218	0.153	0.155

Note: The variables included in highest ranked models from each category (hydraulics, prey, hydraulics + prey, and NREI) are shown in the second column. The ΔAIC_c, model weights, and adjusted r^2 values are shown on the right. The parameter coefficients, standard error (SE), and *p* values of the single highest ranked model (in bold) are shown in the second row of each foraging mode category.

[a]AIC weights represent the represent the relative likelihood of a model being selected and are computed as follows: weights = $\left\{\exp\left[-\frac{1}{2}\Delta_i(\mathrm{AIC})\right]\right\} \Big/ \left\{\sum_{k-1}^{K}\exp\left[-\frac{1}{2}\Delta_k(\mathrm{AIC})\right]\right\}$ (Wagenmakers et al. 2004).

[b]This is the marginal (m) and conditional (c) r^2 following Nakagawa and Schielzeth (2013).

(Supplementary Fig. S7[1]). However, the effects of temperature on critical swimming velocity in *O. mykiss* in California have been shown to be nearly temperature-independent between 10 and 19 °C (Myrick and Cech 2000). The clearest effects of warm water temperature on *O. mykiss* swimming performance and food consumption in California are observed between 19 and 25 °C, when swimming performance, oxygen consumption, and growth rates all tend to decline (Myrick and Cech 2000). Foraging activity of *O. mykiss* in a southern California stream was high between 18 and 20 °C and decreased rapidly above 22 °C (Sloat and Osterback 2013). Daily maximum water temperature during the dates of our video samples did not exceed 18 °C (Fig. 3); therefore, it is unlikely that *O. mykiss* swimming performance and foraging activity were impaired by water temperature in this study.

We also note that body size, which has been shown to be a strong determinant of behavior, was not measured in VidSync during this study and thus not correlated to foraging mode or movement. It is very likely that body size affects foraging movements, aggression, and risk aversion (Brown 1988; Naman et al. 2019). For example, our data showed a similar rate of aggressive interactions from May to August; however, anecdotally we observed more search-foraging YOY engaged in aggressive interactions than drift-foraging parr. Including size-specific foraging data in future VidSync work and incorporating manipulative experiments, like those done by Harvey and White (2017) or Naman et al. (2019), would further resolve the trade-offs among prey concentration, predation risk, and foraging movement rate in *O. mykiss* over the seasonal recession period.

The phenology and drivers of foraging mode

As expected, *O. mykiss* switched from drift- to search-foraging as decreasing water velocity and drifting prey caused increased fish movement during the hydrograph recession. Our mixed effects models show that hydraulic indicators (RCT depth and maximum pool velocity) were much stronger univariate predictors of drift- and search-foraging than the concentration of drifting invertebrate prey. Initially this observation was surprising, because foraging mode shifts have been induced rapidly by experimental reduction of invertebrate drift (Nislow et al. 1998; Fausch et al. 1997). However, while velocity and food concentration interact to mediate the **profitability** of foraging (Fausch 1984; Hughes and Dill 1990), the short-term behavioral response of foraging salmonids to the changes in the physical environment may not completely reflect profitability or fitness. Many fish have been shown to use a spatial sampling process guided by physical cues to develop reliable knowledge of habitat conditions

(Johnson and Rice 2014). Gowan (2007) found that velocity was the primary cue for drift-foraging coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and that dominant fish would not abandon their foraging mode even when food availability was artificially subsidized in a low-risk adjacent habitat. When velocity was manipulated, however, Gowan (2007) observed that fish adapted their behavior and found prey subsidies. While drift concentration was a poor **univariate** predictor of foraging behavior in our study, it was a significant variable in the top-ranked models to predict drift- and search-foraging (Table 3A and 3B). This suggests that (*i*) drift concentration has an additive effect together with hydraulics on fish foraging response and (*ii*) that food (as expected) is an important factor in foraging decisions. However, we tested for interactions in the linear mixed effects models and found no significant interaction terms between hydraulics (velocity and RCT depth) and drift concentration. We suspect that the way food and hydraulics **together** influence behavior may vary nonlinearly as other factors like predation risk and intraspecific competition change seasonally (Harvey and White 2017).

Benthic-foraging was less frequently observed then search-foraging and peaked in late July when it accounted for just over 13% of all foraging observations. Across all pools, we observed over 300 direct attacks on benthic prey, mostly by small young of year *O. mykiss*. Naman et al. (2017) working in British Columbia and Nielsen (1992) working in Washington State also observed very few attacks on the benthos by juvenile salmonids. Merz (2002), working near the southern end of the range of *O. mykiss*, observed juveniles scraping the substrate with their sides and mouths, dislodging algae, which was either ingested by them or other trout close by. We observed a similar behavior in Elder Creek, where juvenile *O. mykiss* would forcefully roll and slap the benthos with their side, before immediately turning to consume any dislodge prey. The increased counts of benthic-foraging we observed in late summer may be associated with both the seasonal decline of hydraulically mediated drift **and** the increasing secondary production on the stream benthos during the streamflow recession. Although we did not sample benthic invertebrate standing crop or renewal rates in pools during this study, we did observe that benthic standing crops in Elder Creek pools peaked a month or more after peak drift flux in 2017 and 2018 (Rossi 2020). Waxing abundance of benthic prey, particularly in late summer when drifting prey are waning, is a potential driver of the increase we observed in benthic-foraging in July (Fig. 5).

Foraging mode and NREI

The statistical associations between hydraulics and prey in top-ranked mixed effects models (for drift- and search-foraging) suggests that an energetics approach, which mechanistically integrates these variables, would be a better predictor of foraging mode shifts. However, our energetics model underperformed in this regard. There are several possible explanations for the weaker response of behavior to NREI, and they suggest some further hypotheses and assumptions that need to be modified about fish behavior and prey fluxes in streams with seasonally low flow and invertebrate drift.

The simplest explanation is that NREI may not correspond to realized energy intake (Hughes et al. 2003), because prey capture and gross energy intake parameters used in the NREI model differed from actual rates experienced by fish in Elder Creek. Drift sampling with passive nets may significantly under-sample the concentration of small drifting taxa (Williams 1985), which would affect realized gross energy intake. Given the preponderance of 1 mm (and smaller) Brachycentridae in our drift samples, this explanation is plausible. Our NREI model also assumed no variation in prey assimilation with temperature, which may have biased our results. Incorporating temperature effects may improve the NREI–behavior linkage. However, summer temperatures in Elder Creek were generally between 10 and 19 °C and average daily temperature remained below 16.5 °C all year. Within this range, assimilation efficiency is expected to change less than 10% (Brocksen and Bugge 1974).

Another possible explanation is the weak correlation between hydraulics and drift concentration and the possible primacy of hydraulics as a cue for *O. mykiss* foraging behavior (Gowan 2007). Although streamflow recession tends to start in early spring as day length begins to increase, differences in prey phenology or in temperature or thermal regimes may drive variability in secondary production of invertebrates. Thus, the hydraulic cues that fish respond to and the food production they are ultimately seeking may vary nonlinearly, with seasonal time dependence in their relationship. Better understanding of the interactions and seasonal offsets of these two drivers (hydraulics and secondary production) would inform future bioenergetic and food web modeling efforts that span seasonal scales. A third explanation for why our NREI model had relatively poor association with foraging mode is that foraging cues provided by the complex 3D hydraulic environment that fish experience were not well reflected in the single focal point velocity used in the NREI model. RCT depth and pool maximum velocity may have been more accurate proxies for changing hydraulic environment (Pasternack et al. 2008; Chiu and Tung 2002) that fish behavior responds to than focal point velocity.

Finally, a fourth possible explanation that our study did not evaluate is the importance of nondrifting invertebrates (e.g., benthos and infall of aquatic and terrestrial prey) for energetic tradeoffs among drift-, search-, and benthic-foraging. The increase of benthic- and search-foraging in late summer may not only reflect declining drift profitability but potentially increasing availability of benthic standing crop and infall of aquatic and terrestrial prey (Rossi 2020). Future efforts to incorporate benthic-foraging into NREI models (as Harvey and Railsback (2014) and Caldwell et al. (2018) did with search-foraging) would advance energetics and behavior modeling in seasonal streams.

Conclusion

The foraging behavior of juvenile salmonids has been the subject of considerable research, but few studies have investigated the drivers or ecological contexts that precipitate different foraging modes. In Elder Creek, we observed more diverse *O. mykiss* foraging behaviors than previously reported for this species. This diversity appears to be triggered by seasonal changes in biotic and abiotic factors during streamflow recession in this Mediterranean-type stream. We found that *O. mykiss* foraging mode could be broadly predicted by hydraulic indicators, except at the very lowest streamflows. However, behavioral theory and the statistical models that best explained our data suggest that prey concentration also influences foraging mode. The interaction between hydraulics and food availability on foraging mode may be nonlinear or mediated by seasonal biotic factors beyond the scope of this study. We recommend that non-drift-related prey fluxes and biotic interactions (especially competition and predator avoidance) be explored in future work on *O. mykiss* behavior in Mediterranean-type streams. The limited effect of water temperature on foraging mode and movement was most likely because maximum temperatures never exceeded thresholds for significant changes *O. mykiss* swimming performance and prey assimilation efficiency. Readers should not infer from this that water temperature would be insignificant in other contexts. Finally, we pose several post hoc hypotheses, based on our data, as to why drift-foraging NREI was a poor predictor of foraging mode and suggest further research to improve NREI models for fish in Mediterranean-type streams.

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