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Seasonal growth potential of *Oncorhynchus mykiss* in streams with contrasting prey phenology and streamflow

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Abstract

The growth of any organism depends on habitat conditions, food availability, and their seasonal interactions. Yet in the vast literature on Pacific salmon (Oncorhynchus), the seasonal interaction between habitat conditions and food availability has received relatively little attention. We examined juvenile Oncorhynchus mykiss rearing, physical habitat, and resource phenologies in two Mediterranean coastal streams-one perennial, cool, and shaded and the other intermittent, seasonally warm, and sunny. We used a bioenergetic model to investigate the timing and magnitude of growth potential for drift-foraging O. mykiss during the spring and summer in both systems. Growth potential peaked at least 2 months earlier in the intermittent stream than in the perennial stream. By early summer (June), growth potential had declined in the intermittent stream, whereas growth rates were peaking in the perennial stream. However, the mid-July lipid content of juvenile O. mykiss in the intermittent stream was nearly twice that of fish in the perennial stream. By late summer (August), foraging profitability declined in both streams, as abiotic conditions in the intermittent stream approached lethal. In contrast, the perennial stream maintained suitable abiotic conditions even though the growth rate was low. We suggest that the divergent resource phenologies and seasonal mortality risks experienced by anadromous O. mykiss rearing in these streams could drive diversification of traits governing size, age, and timing of outmigration.

KEYWORDS

behavior, bioenergetics, flow recession, food webs, growth, lipids, phenology, resource tracking, salmonids, streams

INTRODUCTION

Foragers in seasonally dynamic environments must track fluctuating food resources while avoiding risks and managing metabolic costs that shift through space and time (Dill, 1983; Elton, 1927; Fausch, 1984). Few, if any, habitats are more dynamic than rivers, in which fluctuations in streamflow over diel, seasonal, and interannual timescales drive changing environmental conditions. Streamflows expand, contract, link, and disconnect habitats; and

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periodically reset food webs via bed-scouring floods or dewatering during drought (Power et al., 1988; Trush et al., 2000). This hydrologic variability drives spatial and temporal responses of hydraulic habitat (depth, velocity, and shear stress) and shifts in energy flow, biomass, and biotic interactions in river food webs (Cross et al., 2011; Power & Dietrich, 2002). For foraging predators in streams, the interaction of hydraulic habitat with prey biomass and availability determines their growth potential-the potential energy available for growth under specific contexts of prey availability and energetic costs (Fausch, 1984; Hughes & Dill, 1990). Yet, the seasonal timing of optimal hydraulic conditions for foraging may deviate from the peak of prey availability. Therefore, the seasonal growth potential for predators in river ecosystems must depend on hydraulic habitat dynamics relative to the phenology of prey.

Such interactions are pronounced in streams along the Pacific Coast of California, where aquatic consumers experience Mediterranean hydrologic seasonality and prey phenology. In these systems, the timing and rate of the annual spring-summer streamflow recession relative to seasonal fluctuations in food availability determine growth potential for many aquatic consumers, including Foothill Yellow Legged frog (Rana boylii) (Kupferberg et al., 2011; Railsback et al., 2016), Pacific salmon (Oncorhynchus spp.) (Hayes et al., 2008; Smith & Li, 1983), and benthic macroinvertebrates (Beche et al., 2006; Gasith & Resh, 1999). Characteristic of Mediterranean seasonality, streamflow begins to recede after the last spring rains, following approximate power-law functions (Dralle et al., 2017), and causing nonlinear declines in flow velocity and instream hydraulic complexity. Simultaneously, as days lengthen and flowing water becomes warm and clear, primary (algal and plant) productivity and secondary (invertebrate) productivity increase from spring to early summer, enhancing terrestrial and benthic food supplies for secondary consumers (Gasith & Resh, 1999; Power et al., 2013). In these systems, primary and secondary productivity can decline later in the summer with habitat contraction, thermal stress, and stagnation during late-summer drought (Gasith & Resh, 1999; Hayes et al., 2008; Power et al., 2013; Smith & Li, 1983).

Foraging juvenile salmonids are ideal for studying how the seasonal interaction between hydraulic habitat and prey phenology affects riverine consumers. Extensive mechanistic and bioenergetic modeling has shown how water temperature, stream hydraulics, and prey biomass affect salmonid growth potential (Harvey & Railsback, 2009; Hughes & Dill, 1990; Piccolo et al., 2014). The foraging environment and energetic costs experienced by juvenile salmonids rearing in streams are primarily controlled by stream hydraulics and water quality conditions (Fausch, 1984; Harvey & Railsback, 2009; Nielsen, 1992; Piccolo et al., 2014; Smith & Li, 1983). However, the concentration and quality of prey available for foraging salmonids are determined, in large part, by the phenology of primary and secondary production in streams or donor habitats (Naman et al., 2016; Power & Rainey, 2000; Wipfli & Baxter, 2010). While the interaction between stream hydraulics, water quality, and prey concentration is central to predicting salmonid performance in bioenergetic models (e.g., Dill, 1990; Fausch, 1984; Naman et al., 2019), the seasonal dimensions of these interactions are not well documented in the literature (but see Ebersole et al., 2006; Wipfli & Baxter, 2010).

We investigated the spring through summer hydraulic environment, food web phenology, invertebrate prey dynamics, and growth potential for juvenile steelhead trout (Oncorhynchus mykiss) in two Mediterranean-climate California coastal streams. Both study streams are salmon-bearing and rainfall-dominated systems, but Elder Creek is perennial, cool, and shaded, while Porter Creek is intermittent and seasonally warm, with a more open riparian canopy. We predicted (P1) that waning stream velocity and waxing food availability produce a late-spring or early-summer peak in growth potential for drift-foraging O. mvkiss in both streams, leading to a "dome-shaped" pattern of growth potential across the spring recession (Figure 1; see also Piccolo et al., 2014). This general prediction led to three more predictions about the timing of growth potential:

P2. Growth potential is low during the early-spring recession due to high velocity and low primary and secondary production, leading to low energy intake and high swimming costs;

P3. After a late-spring or early-summer peak, diminishing drift concentrations and increasing metabolic costs during warmer summer months reduce growth potential; and

P4. Growth potential will peak earlier and decline faster in sunnier/warmer Porter Creek than in shadier/colder Elder Creek.

Our study sought to address these predictions and to compare the resource phenologies in these two streams to understand what drives the timing and magnitude of growth potential for *O. mykiss* in both systems.

METHODS

Study sites

Both Elder and Porter Creeks flow through the Northern California Coast Range (Figure 2). Elder Creek is a



FIGURE1 Graphical model of seasonal gradients in hydraulic advection and primary and secondary production during the annual flow recession in Mediterranean streams. These combine to produce earlier peaks in drift flux (dashed line) and later peaks in drift concentration (dotted line) from riffles into pools. Growth opportunity for juvenile salmonids is expected to peak (red box) when stream hydraulics support prey transport and capture and ascending secondary production supports prey biomass. The timing and duration (left-to-right arrows) and magnitude (top-to-bottom arrows) of peak growth potential will vary between streams (or reaches) and years with changing hydraulic advection and secondary production.

16.7-km² tributary of the upper South Fork (SF) Eel River in Mendocino County, California, within the University of California Angelo Coast Range Reserve (39.7181° N, 123.6527° W; Figure 2). Elder Creek's channel is dominated by cobbles and boulders, with streambed gradients ranging from 2% to 5% (McBain and Trush, Trout Unlimited, 2000). The stream is shaded by a dense riparian canopy, primarily comprised of white alder (Alnus *rhombifolia*), with some bigleaf maple (*Acer macrophyllum*) and Oregon ash (Fraxinus latifolia). Elder Creek experiences a characteristic Mediterranean-climate flow recession generally between April and October (Dralle et al., 2017). However, the basin is underlain by deep water-holding argillite shales of the Northern California Coastal Belt, which sustain perennial flow even during prolonged drought (Lovill et al., 2018), so dry season low flows rarely drop below $0.015-0.03 \text{ m}^3/\text{s}$.

Porter Creek is a 19.4-km² tributary to the Russian River in Sonoma County, California (38.5279° N, 122.8992° W; Figure 2). Porter Creek's channel (0.5%–3%) is of lower gradient than Elder Creek's channel with a pebble- and gravel-dominated bed. The riparian community is a mix of alders (*Alnus* spp.), buckeye (*Aesculus californica*), willow (*Salix* spp.), Oregon ash, and coast redwood (*Sequoia sempervirens*), as well as invasive shrubs such as Himalayan blackberry (*Rubus armeniacus*). Except in the wettest years, Porter Creek becomes intermittent during the dry season for much of its length, although the headwaters are typically perennial. The Franciscan mélange geology of the Porter Creek basin (Jennings et al., 1977) has much lower hydraulic infiltration capacity and a shallower Critical Zone than that of the Elder Creek basin, leading to low storage of winter precipitation and greater flow intermittency during the dry summer (Hahm et al., 2019).

Sampling regime

Four riffle-pool habitat units were selected in each stream as study units (Figure 3). The riffle-pool unit is a dominant geomorphic feature in most alluvial streams. During low flow, they can be partially or completely isolated from each other, and so can provide discrete habitats for evaluating juvenile salmonid rearing and foraging (Naman et al., 2018; Rossi, Mierau, & Carah, 2021). We selected riffle-pool units that supported multiple age classes of foraging salmonids and were separated from each other by at least two pools.

We measured the following variables each month between late April and August: (1) streamflow, dissolved oxygen (DO), and water temperature; (2) hydraulics in riffles and pools (depth, velocity, and width); (3) epibenthic primary productivity and algal standing crop; and (4) seasonal invertebrate drift, standing crop, and infall (these data were only collected in three of the four pools in each stream due to sampling constraints). We also captured juvenile *O. mykiss* to estimate growth and lipid content. With these data, we developed a drift-foraging bioenergetic model to predict the seasonal change of *O. mykiss* growth potential in three pools in each stream. Data collection and statistical methods are described below and in Appendices S1–S5.

Seasonal gradients in water quality and stream hydraulics

Streamflow, DO, and water temperature

Streamflow (Q; Table 1) for Elder Creek was retrieved from US Geological Survey gaging station 11475560 "Elder Creek near Branscomb CA," which is 0.6 km upstream from the Elder Creek's confluence with the SF Eel River. All of our Elder Creek study sites were within 0.4 km of this gage, with no intervening tributaries. In Porter Creek, streamflow was retrieved from gaging data collected by



FIGURE 2 Map of study streams and receiving watersheds—Elder Creek, tributary to the South Fork (SF) Eel River in Mendocino County (to the north) and Porter Creek tributary to the Russian River in Sonoma County (to the south). Study reaches are shown in red boxes.

Trout Unlimited, following the methods of Rantz (1982) and California Department of Fish and Wildlife (2013).

DO and water temperature are primary abiotic factors controlling habitat quality for salmonids (Bjornn & Reiser, 1991). We measured DO and stream temperature using continuous HOBO U26 data loggers in one Elder Creek and one Porter Creek pool. The DO loggers were calibrated prior to deployment, and the output data were corrected using the HOBOware Pro's Dissolved Oxygen Assistant software. Calibration measurements were taken monthly using a handheld YSI Pro20. In addition, we collected monthly manual water temperature and DO measurements in each pool when we measured primary productivity using the handheld YSI Pro20. Manual measurements were taken between 11:00 AM and 2:00 PM.

Riffle-pool hydraulics

Measurements of velocity, riffle depth, and width were used to differentiate the seasonal patterns in hydraulics between streams. We installed a cross-stream transect midway through the upstream riffle (XS1), and three cross-stream transects in the downstream pool of each study site. Pool transects were placed where the riffle enters the pool (XS2), a second transect was placed in the pool head patch where



FIGURE 3 Riffle-pool study site design showing representative locations of the transects, drift samples, infall traps (P1-P3), cobble samples (C1-C3), and data loggers.

salmonids were observed to be drift-foraging (XS3), and a third was placed over the maximum depth of the pool (XS4) (Figure 3). Depth and velocity (Table 1) were measured at 0.25-m increments along each cross section. Velocity was measured with a Marsh-McBirney Flo-Mate 2000 electromagnetic flow meter at 0.6 depth from the water surface.

The phenology of O. mykiss prey

Primary production and algal standing crop

In California coastal streams, benthic algae and periphyton are the primary sources of carbon for many benthic invertebrates (Finlay et al., 2002). Thus, seasonal changes in the standing crop of benthic algae affect energy flow to salmon and the phenology of salmon prey abundance. To track the seasonality of primary production, we estimated primary productivity in pools, by measuring net primary productivity and respiration from attached algae on individual cobbles using the light/dark incubation method of Hall and Moll (1975). We estimated benthic algal standing crop using two methods, ash-free dry mass (AFDM) and chlorophyll a (chl a) analysis. We also quantified the presence of filamentous green algae by presence/absence counts on 0.25-m increments along each cross section. Detailed methods for primary production and algal standing crop are described in Appendices S1 and S2, respectively.

Invertebrate drift, standing crop, and infall

To quantify the phenology of invertebrate salmonid prey, we measured invertebrate drift from riffles entering pools, the standing crop of benthic invertebrates on riffle and pool cobbles, and the infall of terrestrial and adult aquatic invertebrates onto the surface of pools. Invertebrates were sampled at six total sites (three Elder Creek pools and three Porter Creek pools) on five dates over the summer. Detailed methods for invertebrate data collection are included in Appendix S3.

All invertebrate samples (drift, standing crop, and infall) were preserved in the field in labeled 50-ml centrifuge tubes filled with 90% ethanol. In the laboratory, drift and benthic samples were sorted and invertebrates identified to family or genus (Merritt & Cummins, 2008) under $10 \times$ magnification. Each invertebrate was measured to the nearest 0.5 mm under a dissecting scope, and biomass (in milligrams of dry mass) was estimated from family- or order-specific length–weight regression analyses (Benke et al., 1999; Sabo et al., 2002). Drift data were used to define prey concentration (in joules per cubic meter) in the bioenergetic model following Rosenfeld and Taylor (2009).

Bioenergetics

The seasonal change in growth potential for drift-foraging *O. mykiss* was estimated using a drift-foraging bioenergetic model (Caldwell et al., 2018; Rosenfeld & Taylor, 2009). The model was developed in R version 3.5.1. and is based on equations from Rosenfeld and Taylor (2009) and Hayes et al. (2000) and is the same model used in Rossi, Power, et al. (2021). Growth potential was inferred from the modeled net rate of energy intake (NREI; in joules per time), estimating the energy acquired by a juvenile fish for growth (gross energy intake – swimming and other metabolic costs). Gross energetic intake is a function of drift

TABLE 1 Study terms and definitions for habitat, invertebrate, and fish variables.

Terms and variables	Definition	Units
Pool head patch	The head of the pool—from where the upstream riffle enters the pool to the maximum pool depth (Figure 3)	m ³
Q	Streamflow	m ³ /s or L ³ /s
Temperature	Water temperature measured at the maximum pool depth	°C
DO	Dissolved oxygen at the pool maximum depth	mg/L
Max depth	Maximum depth at XS3 (e.g., max pool depth)	m
Velocity XS_i	Maximum and mean velocity measured on cross section_i	m/s
Riffle width	Wetted width of flow at XS1 in the upstream riffle	m
Epibenthic photosynthesis	Primary productivity (rate) of benthic algae	$\mathrm{mg}\mathrm{O}_{2}\mathrm{h}^{-1}\mathrm{cm}^{-2}$
Benthic algal standing crop	Biomass of attached algae per stream bed area	mg/cm ²
Drift flux	Mass of invertebrates caught, per hour, in drift net	mg/h
Drift concentration	(Drift flux/discharge through drift net) in the pool head patch estimates mass per volume of invertebrates	mg/m ³
Invertebrate standing crop	Mass of invertebrates per area of the pool bed	mg/cm ²
Invertebrate infall	Mass of invertebrates entering from above per area of pool surface per time	$mg\ m^{-2}\ h^{-1}$
Foraging mode	Counts of observed fish foraging behaviors (drift, search, and benthic foraging)	no.
Foraging movement	Distance that juvenile <i>Oncorhynchus mykiss</i> moved per 3-s interval during computed from VidSync	cm/s
NREI	Net rate of energy intake, modeled for a 100-mm drift-foraging <i>O. mykiss</i> in the pool head patch	J/s
Specific growth	Mass gained in a short interval/starting mass of fish	% Body weight gained per day
Lipids	The percentage of lipid content in muscle tissue of juvenile salmonids (estimated using nonlethal Fatmeter)	%

concentration (in milligrams per cubic meter), discharge rate through the foraging volume, fish size, prey size, and capture probability (Caldwell et al., 2018; Rosenfeld & Taylor, 2009). Swimming costs are a function of fish size and focal point flow velocity and water temperature (Caldwell et al., 2018; Rosenfeld & Taylor, 2009). Water temperature was incorporated into the swimming costs (Rosenfeld & Taylor, 2009); however, we assumed a constant energy assimilation efficiency of 0.6 (Tucker & Rasmussen, 1999). The fish focal point velocity (measured at 6/10ths depth) and drift concentration were measured at the thalweg location on cross section 2 at the head of each pool (Figure 3). This depth was chosen based on our qualitative observations of O. mykiss foraging focal point depth, which was primarily in the lower half of the water column in both streams. We maintained this depth for consistency across the seasons.

We modeled NREI for a 100-mm (fork length) drift-foraging *O. mykiss* at a single foraging location in

the channel thalweg. We considered the head of the pool the best indicator of changing drift-foraging profitability for seasonal comparisons of drift-foraging growth potential across streams (Harvey et al., 2006; Rossi, Power, et al., 2021; Smith & Li, 1983; Van Leeuwen et al., 2011) and 100 mm was representative of the 1+ fish that most commonly occupied the head of the pool. We only modeled one size class of trout since our objective was to model seasonal changes in NREI rather than size-specific growth potential. Caldwell et al. (2018) also noted that NREI for different size classes of drift-foraging O. mykiss and foraging locations downstream from the head of the pool locations followed a similar seasonal pattern over the hydrograph recession, although the magnitudes changed. The model was run for n = 3 pools in each stream, and n = 5 dates for a total of 30 model runs (3 pools \times 2 streams \times 5 dates). Other factors affecting growth potential (e.g., non-drifting prey and impacts from DO) were described qualitatively (see Discussion).

Growth and lipid allocation

Since growth potential (modeled NREI) may differ from realized growth (Hughes et al., 2003; Piccolo et al., 2014), we caught pool-dwelling steelhead to evaluate seasonal changes in the size distributions and fish density, and to collect individual growth and lipid content data. Fish were collected using three-pass backpack electrofishing from three study pools in each stream (Smith-Root backpack electrofisher model LR24). All recaptured fish were remeasured for length and mass, allowing us to estimate June-to-July growth. We did not recapture enough fish during the April-May interval or the July-September interval to estimate growth. In addition to growth, lipid content was estimated using a noninvasive handheld device, the Distell Model 992 Fish Fatmeter (Distellc Inc., West Lothian, Scotland-https://www.distell.com). Lipid allocation in salmonids is used as an indicator of stored energy availability. In O. mykiss, lipid levels have been correlated to survival during periods of resource scarcity (Biro et al., 2004). A detailed description of fish mark and recapture for growth, density, and estimation and lipid estimation is included in Appendix S4.

(Appendix S5: Table S1). Between 10 July and 17 July, streamflow fell to zero in Porter Creek and riffles became dry (Figure 4a). By 9 September, one of the Porter Creek study pools had dried completely, and the other three became shallow and stagnant with 100% mortality of *O. mykiss* that did not migrate prior to disconnectivity (see *Discussion* on life history diversity). In Elder Creek, streamflow continued to decline slowly throughout July and September, reaching a minimum of 0.014 m³/s in early September (Figure 4a).

Mean DO in Elder Creek was near 100% saturation at 10.3 mg/L (SD 0.4) between late April and June, and DO never dropped below 7 mg/L in Elder Creek all summer (Figure 4b). Diurnal variation in DO was also consistent and remained less than 1.5 mg/L throughout the summer (Figure 4b; Appendix S5: Table S1). In Porter Creek, mean DO was 8.8 in June but minimum daily values had fallen as low as 2.1 mg/L (Appendix S5: Table S1), which is a range that can cause significant mortality (Washington State Department of Ecology, 2002). When Porter Creek ceased to flow, daily mean DO dropped rapidly to 5.5 mg/L on 13 July and 4 mg/L on 22 July

Data analysis

We used descriptive statistics to quantify the habitat, food web, and resultant growth potential phenologies for *O. mykiss* in Elder and Porter Creek and to compare seasonal trends in both streams against our directional predictions. We also compared these seasonal patterns against our graphical model (Figure 1). In addition, we used a post hoc bioenergetic analysis to evaluate our predictions about the trends and drivers of modeled seasonal growth potential (1–4). We extracted the modeled swimming costs and energy intake to determine their seasonal variance and relative influence on patterns of growth potential.

RESULTS

Seasonal gradients in water quality and stream hydraulics

Streamflow, DO, and water temperature

Streamflow declined in both streams across the study period (late April to September) but was always lower and declined much faster in Porter Creek (Figure 4a). The daily average streamflow of Elder Creek in April (1322 L/s) was 3.5 times higher than that of Porter Creek (373.5 L/s) increasing to 16.5 times higher by July



FIGURE 4 Continuous daily average streamflow (a) and hourly dissolved oxygen (b), and hourly water temperature (c) in Elder and Porter Creeks. The dashed red line shows the period during which riffles and pool first disconnected in Porter Creek (10–17 July). This pool dried entirely in mid-September.

(Figure 4b), which is below levels shown to impair swimming performance and food conversion efficiency for juvenile *O. mykiss* (Bjornn & Reiser, 1991). Daily average water temperature increased in both streams from April to peak in mid-July (Figure 4c). The average daily water temperature was 2.9°C (SD 1.25) cooler in Elder Creek than in Porter Creek throughout the summer (Appendix S5: Table S1). The mean July water temperature was 16.6° C (SD 1.4) in Elder Creek and 18.9° C in Porter Creek (SD 1.4). However, daily peak temperatures in August and September exceeded 30° C in Porter Creek, which was identified as a threshold for summer *O. mykiss* persistence in southern California (Sloat & Osterback, 2013). In contrast, daily peak temperatures remained below 21°C in Elder Creek all summer (Appendix S5: Table S1).

Riffle-pool hydraulics

Pool depth declined at a similar rate in both streams, decreasing an average of 21% between late April and August in Elder Creek and 27% in Porter Creek over the same period (Figure 5a; Appendix S5: Table S1). One Porter Creek pool dried completely during this period. Maximum pool velocities were an average of 2.96 times higher in



FIGURE 5 (a-d) Spring and summer changes in hydraulic variables in Elder Creek (black) and Porter Creek (gray). (e-h) Spring and summer changes in measures of epibenthic photosynthesis, benthic algal standing crop, and observations of filamentous green algae. Boxplots are connected at median net rate of energy intake values, boxes show 25%–75% quartile range, and whiskers show the 95% percentile range.

Elder Creek than in Porter Creek over the whole summer (Appendix S5: Table S1). Pool velocity declined at a slower rate in Elder Creek, from a mean of 0.24 m/s (SD 0.33) in late April to a mean of 0.07 m/s (SD 0.7) in August, than in Porter Creek, from a mean of 0.09 m/s (SD 0.15) in late April to a mean of 0 m/s (SD 0.0) in August (Figure 5b; Appendix S5: Table S1). Wetted riffle widths declined by 30% between late April and June in Elder Creek, but the rate of decline was less than 7% from July to August, whereas in Porter Creek, riffle widths declined by 47% between late April and throughout July and riffles dried completely between 10 July and 17 July (Appendix S5: Table S1; Figure 5c). Riffle depth (Figure 5d) also declined in both streams following power-law trends. In Elder Creek, average riffle depth dropped from a median of 0.18 m in late April to 0.06 m in August, whereas in Porter Creek, the median average riffle depth declined from 0.09 m in late April to 0.05 m on 10 July, before rapidly declining from 0.05 to 0 m on 17 July (Figure 5d).

The phenology of O. mykiss prey

Epibenthic photosynthesis and algal standing crop

Average rates of epibenthic photosynthesis were 2.6 times higher in Porter Creek (mean 5.42 mg O_2 h⁻¹ cm⁻², SD 3.58) than in Elder Creek (mean 2.06 mg O_2 h⁻¹ cm⁻², SD 1.72) over the summer (Appendix S5: Table S1), and the seasonal patterns of photosynthesis were also distinct between the two streams (Figure 5e). In Elder Creek, epibenthic photosynthetic rates increased from late April to June and decreased from June to August (Figure 5e). Conversely, in Porter Creek, average epibenthic photosynthesis decreased from late April to May and increased slightly in June before jumping by a factor 2.8 in July and August—after riffle-pool disconnectivity (Figure 5e). Benthic algal standing crop, both AFDM and chl a, followed similar patterns to photosynthesis; however, chl a in Porter Creek continued to increase through August (Figure 5f,g). Filamentous green *Cladophora* biomass peaked in May in Elder Creek and in June in Porter Creek, although Cladophora rebounded in July and August in Elder Creek, whereas it senesced and decayed in Porter Creek during July (Figure 5h).

Invertebrate drift, standing crop, and infall

After removing individuals >12 mm, which made up <0.5% of total numbers, the total measured (time- and area-averaged) biomass of drifting invertebrates between late

April and August was 439.69 mg in Elder Creek and 352.76 mg in Porter Creek. While these numbers are similar, the phenology of drifting invertebrate biomass was distinct between streams (Figure 6a,b). During late April, the average drifting invertebrate flux was more than twice as high in Porter Creek (115.7 mg/h, SD 89.8) than in Elder Creek (54.7 mg/h, SD 64.8), and drift concentration was 11 times greater in Porter Creek (0.1 mg/m³, SD 0.05) than in Elder Creek (1.1 mg/m³, SD 0.4) (Appendix S5: Table S1). This scenario was reversed in May when the average drift flux of Elder Creek (143 mg/h, SD 108.2) was 10 times greater than that of Porter Creek (14.6 mg/h, SD 24.6), and in June where drift concentration was 2.25 greater in Elder (0.9 mg/m³, SD 0.4) than in Porter Creek (0.4 mg/m³, SD 0.1).

Benthic invertebrate standing crop on pool cobbles had near-diametrically opposite patterns in Porter and Elder Creek between late April and August (Figure 6c). Like drift concentration, Elder Creek invertebrate standing crop increased sharply from late April to June (mean June standing crop 814 mg/m², SD 540.6), before decreasing in July and increasing slightly in August (Figure 6c; Appendix S5: Table S1). Porter Creek invertebrate standing crop was highest in late April (mean 1184 mg/m², SD 1036), decreasing sharply to June before increasing in July and August (Figure 6c; Appendix S5: Table S1).

Unlike drift and standing crop, infall of terrestrial and adult aquatic invertebrates followed a similar seasonal pattern and magnitude in both streams—although late-April infall in Porter Creek (mean 16.4 mg m⁻² h⁻¹, SD 16.2) was much higher than in Elder Creek (mean 1.3 mg m⁻² h⁻¹, SD 2.2) (Figure 6d; Appendix S5: Table S1). Both streams saw an increase in infall between May and July (Figure 6d). Infall decreased sharply from July to August in Porter Creek while only declining moderately in Elder.

O. mykiss bioenergetics, movement, growth, and lipid allocation

Bioenergetics

Consistent with predictions P1 and P2, Elder Creek modeled swimming costs decreased (although only slightly) from late April to June, while modeled energy intake increased (Table 2) leading to peak growth potential in June (Figure 7). Swimming costs increased again during July and August (due to warmer water temperatures), and drift concentration declined rapidly during this same period, leading to low NREI (P3). However, contrary to P1 and P2, modeled energy intake in Porter Creek was highest and swimming costs were lowest in late April (Table 2), producing the highest modeled NREI (Figure 7). Growth potential in Porter Creek declined sharply from late April to



FIGURE 6 Seasonal gradients of drifting invertebrate flux (a) and concentration (b), invertebrate benthic standing crop (c), and invertebrate infall (d) in Elder Creek (black) and Porter Creek (gray) pools. The dashed box represents a 1-m³ volume of drift concentration in the pool head patch, which was applied to the drift-foraging volume in the net rate of energy intake model (see *Methods*). Boxplots are connected at median values, boxes show 25%–75% quartile range, and whiskers show the 95% percentile range.

TABLE 2	Mean swimming costs (in joules per second), energy intake (in joules per second), and the difference (intake - costs)
computed from	n the Elder Creek and Porter Creek bioenergetic models during the spring and summer of 2018.

	Elder Creek			Porter Creek		
Period	Swimming costs	Energy intake	Intake – costs	Swimming costs	Energy intake	Intake – costs
Late April	0.01	0.047	0.037	0.009	0.175	0.166
May	0.01	0.158	0.148	0.013	0.047	0.034
June	0.009	0.132	0.123	0.016	0.026	0.01
July	0.011	0.021	0.01	0.015	0.01	-0.005
August	0.011	0.013	0.002	0.014	0	-0.014



FIGURE 7 Modeled net rate of energy intake (NREI) for a 100-mm drift-foraging *Oncorhynchus mykiss*, at the head of three pools in Porter Creek (gray) and three pools in Elder Creek (black). Boxplots are connected at median NREI values, boxes show 25%–75% quartile range, and whiskers show the 95% percentile range.

June with negative NREI in July and August. This supports Prediction 4: that Porter Creek has an earlier onset of profitable foraging habitat and a longer duration of inhospitable conditions during the summer than Elder Creek. Porter Creek's peak NREI (in late April) was higher than Elder Creek's peak NREI (in June); however, the duration of positive NREI between 28 April and 10 August was nearly twice as long in Elder Creek as in Porter Creek (Figure 7).

Growth and lipid content

Most recaptured O. mykiss in Elder and Porter Creeks gained mass between 1 June and 17 July, despite the drift-foraging energetic model predicting that a 100-mm O. mykiss would lose mass in Porter Creek during this period. In fact, only 4 of 21 Porter recaptures lost mass (Figure 8a), while zero of the eight recaptured fish in Elder Creek lost mass. Between June and July, median specific growth rate was three times higher for Elder Creek (0.6%/day) than for Porter Creek (0.2%/day). No growth data were collected during the April and May periods. The limited number of recaptures in September all showed zero or negative growth rates over this period (Appendix S4: Figure S1). All Porter Creek salmonids had either emigrated from our study pools or perished by September (Appendix S4: Figure S2; see Discussion on life history diversity). Lipid content, measured only in mid-July, was nearly two times higher in Porter Creek (mean 4.4%, SD 1.58) than in Elder Creek (mean 2.4%, SD 1.0) (Figure 8b).



FIGURE 8 (a) Specific growth rate (SGR) of juvenile
Oncorhynchus mykiss between 1 June and 17 July from Elder Creek (8 individuals, black) and Porter Creek (21 individuals, gray).
(b) Measured lipid content in muscle tissue of juvenile O. mykiss in mid-July from 81 fish in Elder Creek and 67 fish in Porter Creek.

DISCUSSION

Elder Creek (perennial, shaded, and cool) and Porter Creek (intermittent, sunny, and seasonally warm) represent nearly opposite ends of a hydrologic spectrum of Mediterranean streams. Our study shows that seasonal differences in pool hydraulics, prey phenologies, and patterns of O. mykiss growth potential reflect the hydrologic, energetic, and geomorphic differences between these two systems. Both Elder and Porter Creek offered profitable foraging opportunities for pool-dwelling O. mykiss during the spring and summer of 2018 but at different times. Prey concentration and drift-foraging profitability peaked at least 2 months earlier in Porter Creek than in Elder Creek. Late-summer abiotic conditions in Porter Creek (drying pools, low DO, and high temperature) were also much harsher than those in Elder Creek. In addition, we suggest that the profitability of salmonid foraging in both streams, while driven by stream-specific seasonal changes in food and habitat, was modulated by flexibility in foraging modes. The distinct seasonality of growth potential and summer habitat in these contrasting stream types suggests that they could both contribute to the regional portfolio of juvenile salmonid life histories (Schindler et al., 2010), selecting for site-specific differences in growth, in timing of outmigration (mean and duration), and in the age, size, and physiological complexity of out-migrating fish.

The seasonality of *O. mykiss* growth opportunity

Seasonal change in the gross rate of energy intake was the primary driver of growth potential in both streams (Table 2, Figure 7). Over the study period, energy intake varied by a factor of 16 in Porter Creek and by a factor of 12 in Elder Creek. In contrast, maximum swimming costs over the study period were less than twice the minimum swimming costs in both streams (Table 2). Gross energy intake was driven by invertebrate drift concentration and water temperature. While velocity drove slightly higher swimming costs in late April in Elder Creek, metabolic costs for most of the study period were primarily driven by water temperature.

Why did drift concentration and water temperature differ between these two streams? Greater sunlight penetration and an earlier and faster streamflow recession in Porter Creek led to earlier warming and a pulse of autochthonous primary production prior to late April. This earlier growth of attached algae in Porter Creek could then fuel invertebrate production (Vadeboncoeur & Power, 2017), leading to the high drift concentrations (mostly from aquatic origin taxa) that we observed in late April. In Elder Creek, in contrast, extended streamflow recession, colder water (10°C in April), and a dense riparian canopy delayed high rates of epibenthic photosynthesis until May, which led to the hump-shaped pattern of aquatic invertebrate biomass (Figure 6). While the effect of allochthonous carbon sources was not quantified in this study, terrestrial invertebrate biomass in the drift was low in both streams (2% in Elder and 1.8% in Porter). However, the proportion of terrestrial invertebrates in the infall was higher than in the drift, and similar in Porter (43%) and Elder (38%) Creeks. Terrestrial invertebrates may have been more important for the growth of young-of-year (YOY) O. mykiss, who were more likely to be search foragers and surface feeders (Rossi, 2020; Rossi, Power, et al., 2021).

As predicted (P1), the average flux of drifting prey peaked earlier than concentration in Elder Creek, while both flux and concentration declined from late April to July in Porter Creek before flow and drift ceased entirely in July 2018. Increased invertebrate infall in mid-summer, after drift and standing crop declined, may have provided an important asynchronous prey subsidy for salmonids, as demonstrated by Nakano and Murakami (2001) for a more seasonally offset continental-climate stream ecosystem.

The behavioral and ecological drivers of "realized" O. mykiss foraging profitability

Although we recaptured relatively few fish (8 in Elder Creek and 21 in Porter Creek), the observation of mostly

positive growth in Porter Creek between June and July was not consistent with the NREI model, which predicted negative energetic intake during that period. Furthermore, it is likely that our model assumptions overpredicted drift-foraging NREI for many fish in Porter Creek at very low flow. For example, we modeled prey capture success as a function of water velocity and prey size based on laboratory studies (e.g., Hill & Grossman, 1993). But our model assumed fish always experienced mid-column water velocity at the head of the pool, which is not realistic, particularly for subordinate fish (Nielsen, 1992). This choice likely overpredicted prey capture success in Porter Creek, since near-zero velocities elsewhere in the pool would have decreased model capture success (Hill & Grossman, 1993). We observed many smaller fish utilizing portions of the study pools that had zero or near-zero velocities in Porter Creek. In addition, low DO in June and July, and significantly higher fish density in Porter Creek than in Elder Creek (Appendix S4: Table S1) may indicate further impairment of realized growth potential (Bjornn & Reiser, 1991; Grant & Imre, 2005).

Why were measured growth rates so much higher than predicted by the model? The most likely explanation for the positive growth rate in Porter Creek is that fish profited from non-drift-foraging behaviors (e.g., search, benthic, or surface foraging) that were not considered in the NREI model (Rossi, Power, et al., 2021). While snorkeling, we observed that downstream positions (near the tail of the pool) were more commonly occupied by search-foraging YOY fish. Most recaptured YOY (15 of 17) experienced positive growth between June and July in Porter Creek. Rossi (2020) observed that YOY salmonids engaged in significant non-drift-foraging behavior in Porter Creek (>50% of observations during the summer), which was consistent with our observations in this study. Based on these lines of evidence, it appears likely that fish, especially subdominant individuals, were benefiting energetically from non-drift-related foraging in June and July. These findings highlight the challenge of capture success estimation in bioenergetic models for drift-foraging fish that employ other feeding strategies at high densities and/or low velocities (Piccolo et al., 2014; Rosenfeld et al., 2014).

Bioenergetic considerations for future work

Our NREI model for drift foraging at the head of the pool was far from an exhaustive treatment of the pool-scale profitability for salmonids foraging in Elder and Porter Creeks. Further study of the energetic profitability of search, surface, and benthic foraging that links these

modes to non-drift-related prey fluxes foraging (Nielsen, 1992) would greatly improve our ability to preunder dict salmonid fitness variable natural (or managed) flow regimes, especially in streams with strongly seasonal drift patterns (Caldwell et al., 2018; Fausch et al., 1997; Harvey & Railsback, 2014; Nislow et al., 1998). Movement data computed from programs such as VidSync (Neuswanger et al., 2016) could be used to refine swimming cost equation in energetic models, particularly for search-foraging fish, actively swimming through the water column. However, incorporating non-drift-related prey fluxes would require more than refining existing drift-foraging models, but a compressive assessment of search-foraging dynamics. Most NREI models currently assume swimming costs are proportional to focal point velocity (Rosenfeld & Taylor, 2009), which is incorrect for actively swimming animals (Harvey & Railsback, 2014). Harvey and Railsback (2014) incorporated "velocity shelters" into swimming costs for search foragers, but they did not use measured swimming speeds. In addition, VidSync data can provide critical information on occupied foraging volumes, which is a key area of uncertainty in search-foraging models (Harvey & Railsback, 2014).

Life history diversity in streams with contrasting prey phenology and streamflow recessions

In Atlantic salmon, lipid levels predict early migration (Morgan et al., 2002), and summer lipids correlate with the survival of O. mykiss under harsh winter conditions (Biro et al., 2004). Porter Creek O. mykiss had nearly twice the July muscle lipid content as Elder Creek O. mykiss, even after riffle-pool disconnection. This was probably due to higher feeding rates in early spring in Porter Creek; however, we cannot rule out lipid allocation as an adaption to early migration or harsh summer conditions in Porter Creek. Profitable early-spring growth potential, inhospitable late-summer abiotic conditions, and low over-summer survival (Obedzinski, 2020, personal communication) may favor YOY emigration to non-natal rearing habitat (e.g., mainstem or estuarine habitat) as a life history adaptation to stream drying in streams such as Porter Creek (Erman & Hawthorne, 1976; Hayes et al., 2008).

The total number of salmonids that successfully migrated out of Porter Creek before it disconnected is unknown, but 9 of 82 salmonids tagged in Porter Creek in June 2018 were detected emigrating the following spring (2019) through paired antennas near the mouth of Porter Creek (UC Sea Grant, 2020, unpublished data). In 2019, a much wetter summer, 33 of 100 salmonids tagged in June were observed at the mouth of Porter Creek either that winter (December 2019) or during the following spring (2020) (UC Sea Grant, 2020, unpublished data). These and other data suggest that over-summer survival likely varies significantly with the annual hydrology in Porter Creek. A key unknown is the fate of migratory YOY, which were too small to PIT-tag in May or June.

In contrast to the patterns observed in intermittent Porter Creek, Kelson and Carlson (2019) showed that outmigration timing and late-summer densities of O. mykiss in Elder Creek remained relatively constant across dry and wet water years. High growth potential in spring and early summer, and lower apparent summer mortality suggest that over-summering of fish expressing both anadromous and resident life histories would be favored in Elder Creek, in contrast to Porter Creek. Life cycle monitoring along with energetics and growth data from many streams would be necessary to test these conjectures. However, differences in the phenology of food webs that feed O. mykiss, along with late-summer survival potential, indicate that selective pressures on traits including size, age, physiology, and timing of O. mykiss at outmigration could diversify life histories across streams, potentially stabilizing salmon populations along California's North Coast.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Rossi, 2022) are available from Dryad: https://doi. org/10.6078/D1TM66.

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SUPPORTING INFORMATION

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

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