

Bioenergetics of Juvenile Salmonid Foraging: a Mediterranean Stream Case Study

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ABSTRACT

Bioenergetics, in a broader ecological context, is the study of energy relationships and energy transformations in organisms. I adapted a pre-existing bioenergetics model for juvenile coho salmon and juvenile steelhead trout, to account for an alternative form of foraging (search foraging, a previously understudied strategy for obtaining calories in fish) in a Northern-California Mediterranean climate stream. I calculated how the energetic profitabilities of different foraging modes (both drift foraging and search foraging) changed throughout the summer as flow decreased, water temperature increased, and dissolved oxygen decreased. I found that it was more energetically beneficial for the juvenile salmonid fish to search forage in the summer months, and I observed a significant increase in the percentage of search foraging behavioral events as the summer went on. The fish are hypothesized to be able to evaluate the relative energetic profitabilities of each foraging mode and are also able to change their behavior accordingly. These results have the potential to inform conservation and management of Mediterranean streams, as well as improving the accuracy of existing bioenergetics models.

KEYWORDS

aquatic ecology, fish conservation, streamflow, foraging behavior, ecological modeling

INTRODUCTION

The abiotic and biotic variables that constitute aquatic stream habitats affect the health of stream-dwelling fishes in significant and complex ways. Habitat structure and prey composition are two major variables that influence realized growth and survival rates of juvenile salmonids (Rosenfeld & Taylor 2009). Juvenile salmonids choose spots in the stream that maximize their net energy intake (NEI), defined as the amount of calories consumed minus the calories expended foraging and calories burned via respiration (Fausch 1984), and this tendency to maximize NEI is essential for the survival and growth of the fish. Key variables that impact NEI include abundance and size of macroinvertebrates, stream velocity, temperature, and dissolved oxygen, to name a few (Naman et al. 2018). On an individual basis, the fish perform foraging behaviors that allow them to maximize the amount of food that they eat, while minimizing swimming costs and metabolic costs. In the Mediterranean streams of Northern California, maximizing the fish's net energy intake depends on unique environmental constraints of the stream, so establishing accurate relationships between these environmental variables and fish behavior is essential to inform restoration of these ecosystems.

One of Northern California's emblematic Mediterranean watersheds is the Russian River Watershed, which encompasses 1,485 square miles of land and contains approximately 238 streams and creeks that support local fish species ("Russian River Watershed Association" 2019). These streams have a Mediterranean hydrologic regime, which means that all precipitation is condensed within the course of a few days within the winter, and the summers are warm and dry (Gasith & Resh 1999). Mediterranean hydrologic regimes start off in the spring with high flow but have no additional inputs of water throughout the summer so the flows decrease to essentially zero in the late summer months (Cid et al. 2017), which has energetic implications for the fish that live in these streams.

The Russian River Watershed is habitat to two ecologically and economically important salmonid species: Coho Salmon (*Oncorhynchus kisutch*) and Steelhead Trout (*Oncorhynchus mykiss*), both of which spend significant portions of their lives in these streams. California's Central Coast has one of the most vulnerable coho populations in the world, and in this region the coho salmon is locally listed as endangered ("NOAA Central California Coast Coho" 2005). Steelhead trout are listed as threatened in California's Central Coast ("NOAA Endangered and

Threatened Species” 2006), so intense conservation of both species is required to restore their populations to healthy and sustainable levels. Both species have anadromous life histories, swimming from the Pacific Ocean into freshwater streams to spawn, because the freshwater tributaries have more readily accessible nutrients for the fry and fewer aquatic predators (Wiginton Jr. et al. 2006). Once the eggs hatch, the salmonids remain in the freshwater stream for about a year on average (Obiedzinski 2018), in an effort to grow large enough to survive in the open ocean. Salmonid survival in marine and estuarine ecosystems is strongly correlated with length of the fish (Grantham et al. 2012), so optimizing growth is essential while in these Mediterranean freshwater streams. Growth optimization can only be done by maximizing the amount of calories consumed and minimizing the amount of calories lost. The relationship between the variables that influence fish growth are measured by using bioenergetics models.

Bioenergetics models have been used frequently in rivers and higher flow streams (Railsback & Harvey, 2002; Rosenfeld & Taylor 2009, Piccolo et al. 2014), but there have been far fewer studies that apply these models to intermittent streams with phenological components to them (Caldwell & Chandra 2018). These models do not take into account the changing flows of these Mediterranean streams, so the models must be adapted and revised to account for the phenomenological changes in streamflow (Railsback & Harvey 2009). At the beginning of the summer, streamflows are usually sufficient to bring drifting macroinvertebrates into the pools, so the least energy-intensive foraging strategy for salmonids is to swim in a stationary spot at the head of the pool and make quick forays to eat the bugs as they drift past, then returning to their original location (*drift foraging*) (Railsback & Harvey 2014). However, as the flows decrease more and more, the fish are forced to resort to more energy-intensive foraging methods in order to obtain food (*search foraging*), which consists of actively searching for food floating on the surface, eating the drift that is settling at the back of the pool, or searching for food on the benthos (Naman et al. 2019). Very few models have taken search foraging into account, because it is assumed that drift foraging is always an option, and always more energy-efficient.

The primary purpose of this study is to create a bioenergetics model for the salmonids that takes the Mediterranean hydrological regime into account by incorporating alternative modes of foraging other than drift foraging. I analyzed data from Porter Creek, a representative Mediterranean stream that seasonally disconnects from the main stem of the Russian River, to answer three main questions about accounting for a Mediterranean stream’s phenology within a

bioenergetics model. First, how do the energetic profitabilities of each foraging mode change throughout the season as the flows decrease? Previous studies have focused on only drift foraging (Naman et al. 2019), because it is the most efficient method of foraging, but this method of foraging might not be realistic in the low-flow late summer months. Second, are the changes in foraging mode correlated with changes in caloric content of each flux? To answer this question, I gathered data from each source of food for the salmonids (drift food, benthic food, and surface food) in a certain amount of time in order to get three fluxes of food for the fish. Using species-specific biomass regressions for macroinvertebrates (Safit 2003), I calculated the percentage of calories available to the fish from each food source to determine if that is the main determinant of a fish's foraging strategy or if other factors are at play, which brings us to my last question: What variables influence a fish's decision to switch foraging modes? I attempted to answer this question by combining environmental and behavioral variables to assess and quantify fish responses.

METHODS

Study site

This study focuses on Porter Creek, a small (approximately 7 continuous miles) second order stream that is connected to the Russian River in the early summer, and then becomes disconnected in late summer due to the Mediterranean dry summer conditions and groundwater infiltration. The bedrock in the lower part of the creek is much more porous, which causes water to permeate into groundwater deposits. In the late summer – when flows are lowest – the lower portion of the creek becomes disconnected from the main channel of the river, therefore trapping all aquatic animals within the creek until the next precipitation event that is sufficiently large to connect the creek with the main channel of the Russian River. In this amount of time, the fish have to maximize their NEI to survive (Obedzinski et al. 2018).

I chose three main pools on the stream to analyze that represented the diversity in flow regimes of a Mediterranean stream. The pools (titled 18.2, 18.3, and 18.4; Figure 1) were originally part of a larger (not yet published) study that focused on flow augmentation, but I chose these pools from the control group to show how the fish react to the variables associated with the

unaugmented flow of the stream. The study that focused on flow augmentation did not affect these selected pools in any of the variables that will be used in the bioenergetics modeling.

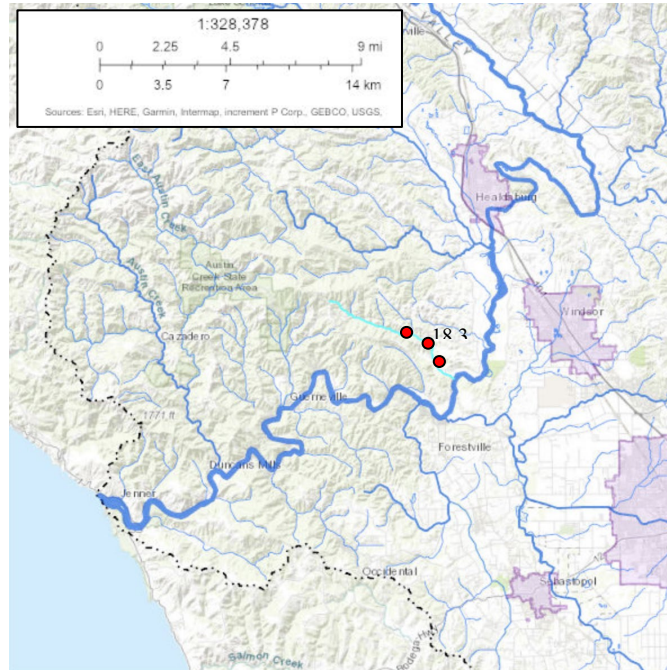


Figure 1: A map of Porter Creek, showing the three selected pools for analysis.

Abiotic Habitat Data Collection Methods

One of the major goals of bioenergetics models is to link fish behavior to its physical environment, so our team (Gabriel Rossi, primary researcher; Shelley Pneh, bug taxonomist; Shannon McKillop-Herr; field technician; and myself, field technician) measured changes in water temperature, velocity, dissolved oxygen, and riffle-crest trough depth for each of the pools. We measured how these variables were changing throughout the summer as the flow declined, which would then allow us to correlate that with fish growth.

We measured velocity using a Marsh-McBirney® Flo-Mate 200 Stream Flow Meter, taken immediately after we took out the drift nets for macroinvertebrate sampling. We measured velocity at the site of the drift net, then 1 meter downstream, 2 meters downstream, then 3 meters downstream to determine how velocity decreases throughout each pool. I measured riffle crest thalweg depth (RCT), which is the deepest part of the riffle crest (the riffle crest is the “V-shaped” curve that forms in the river channel at the beginning of the riffle) at the front of the pool to

determine the relationship between pool volume and flow. HOBO Data loggers installed in each pool measured the rest of the abiotic parameters. The loggers were attached to rebar pins in the deepest part of each pool, and each data logger takes hourly measurements of water temperature (degrees Fahrenheit), dissolved oxygen (ppm), and pool depth (cm) throughout the summer.

Macroinvertebrate Fluxes

To determine how the macroinvertebrate biomass fluxes changed throughout the summer, I collected the rates at which they were entering the freshwater systems at various points throughout the summer. We sampled each flux at five different times throughout the summer, comparing the calories available from each invertebrate flux at a given time period.

Drift Flux

To sample for the number of macroinvertebrates entering each pool over either one or two hours, I used drift nets placed for approximately 1-2 hours at the highest velocity section at the upstream section of the pool. The net captured all the macroinvertebrates that were being carried into this cross section of the pool in the flow in units of milligrams of biomass per second. I measured the height difference between the water level and the top of the drift net's frame so that I would be able to determine how concentrated the drift was within the water column. I also made notes of fish presence or absence within each drift net once it was taken out, because this might have artificially lowered the levels of macroinvertebrates due to predation.

Benthic Flux

To measure the benthic flux of macroinvertebrates from the substrate within each pool, I and the other field technician filled 'cobble baskets' with the representative substrate and measured the recruitment rate of macroinvertebrates (milligrams of biomass per time). Each pool had 3 cobble baskets, with one placed in the upstream third of the pool, one within the middle third, and one within the downstream end. I measured the rock sizes using a Wildco® Gravelometer Field Sieve. The cobble baskets were made out of chicken wire, with the dimensions as follows:

Radius = 7.5cm, Cell size = 1cm x 1cm, Height = 15cm (but only filled 8cm high)

I filled each rock basket with the representative substrate of each section, making sure to fill the basket 8cm high with rocks. Once we had chosen the representative rocks and put them into their respective baskets, we then elutriated the rocks to remove any macroinvertebrates on the rocks. To do this, we put the rocks in a bucket, filled it a quarter of the way with water, and shook it aggressively. This procedure was repeated five times. Afterwards, we sorted through each rock to manually check for any leftover macroinvertebrates still attached to the bucket or rocks (this method was necessary for finding and removing most of the snails, because elutriation was not as effective at removing them). This blank cobble basket is the starting point for the macroinvertebrates colonization. We left the baskets for two weeks, then we elutriated again, but this time we filtered the macroinvertebrates and stored them in 95% ethanol for laboratory analysis.

Surface Flux

To measure the contributions of biomass from the terrestrial environment, I measured the rate at which terrestrial insects fell into pan traps laid around each of the pools. I placed three pan traps placed on the shore alongside each of the pools, making sure to maximize the space between each pan trap and not setting the pan traps underneath vegetation. The pan traps consisted of a plastic bin (dimensions: 22cm x 22cm x 10cm) filled about a fourth of the way full with water, then adding approximately 1ml of soap to the trap to break the surface tension. I left each trap for approximately 48 hours and then identified the taxa to the family level and recorded the length of each macroinvertebrate in the field.

Fish Growth

We PIT-tagged approximately 50 fish of multiple species that were of a sufficient size at the beginning of the summer to track the movements of the fish, but this also allowed us to track the growth of each individual fish when we caught it in later electrofishing events. Throughout the summer, there were four electrofishing events, which presented opportunities for PIT-tagging new fish, measuring and weighing fish, and tracking the growth rates of the previously tagged fish. Electrofishing was conducted on a pool-by-pool basis and consisted of first setting up nets at the

downstream and upstream ends to ensure that we obtained accurate fish data for each pool. Then, one or two electrofishers would sweep up and down the pool with at least three netters grabbing the stunned fish. Some pools had more hiding areas for the fish, so more sweeps were needed to get a capture rate of at least 90%. In the first three electrofishing events, our team (both UC Berkeley researchers and employees of California SeaGrant) PIT-tagged fish that were at least 58mm long (nose to tail fork). We prioritized PIT-tagging coho and steelhead, but we also tagged some California roach and sculpin to assess competition for food in pools.

We were able to associate each PIT tag with the fish's measurements, so we were able to track both their growth throughout the season and migration, due to our sensors placed throughout the stream. SeaGrant had antennae sensors lying across the entire width of the stream in between each pool, so when PIT-tagged fish swam underneath it, it would register the particular fish. This allowed us to measure the emigration and immigration rates of fish throughout the summer, which allowed us to determine which pools the tagged fish spent the most amount of time in.

Calculation of Net Rate of Energy Intake

Converting Biomass into Energy

To evaluate the biomass of each food flux, I manually sorted through each sample and measured the length of each individual macroinvertebrate (although usually only identified to family level), and then calculated biomass using biomass regression tables. I used a dissecting scope to identify macroinvertebrates from each sample to the highest possible taxonomic resolution, which I then confirmed with a professional insect taxonomist. The data was entered into an equation that uses the length and species for taxon-specific caloric density equations from previous literature (Smock 1980, Sabo et al. 2002, Benke et al. 1999). These series of equations allowed me to convert length measurements of a particular macroinvertebrate to biomass, then biomass to energy content. This equation in the following equations was assigned the variable name `Joules_per_m3`, shown in the following equations.

Energy Intake Equations

To measure drift foraging, I used the foraging model of Harvey and Railsback (2009) that modeled net energy intake of drift foragers:

$$\text{Drift_Intake} = \text{Capture_Success} * \text{Biomass_Volume} * \text{Joules_per_m3} * \text{Handling_Loss}$$

Capture Success = the percentage of successful drift forays a fish of a certain size class makes (success measured by ingested prey).

Biomass Volume = The volume of prey for a fish at a certain velocity (m^3/second).

Joules per m3: Calculating the energy density of the macroinvertebrate biomass.

Handling Loss: Accounting for the time expended between the time the fish notices the prey and eats the prey.

To measure the search foraging of fish, I modified the pre-existing bioenergetics model InSTREAM (Harvey & Railsback 2009). This equation was originally only for drift foragers, so I modified it for search foraging. It is important to note that the variables for this equation are generalized, and not calculated in the same way that the drift foraging variables were calculated. The general equation is as follows:

$$\text{Search_Intake} = \text{Biomass_Volume} * (1 - \text{Velocity}/\text{Velocity_Max}) * \text{Joules_per_m3}$$

Biomass Volume = The volume of prey for a fish at a certain velocity (m^3/second).

Velocity = The velocity felt by a fish of a certain size class (cm/sec).

Velocity Max = The maximum velocity that a fish of a certain size class could swim in for an extended period of time (cm/sec).

Joules per m3: Calculating the energy density of the macroinvertebrate biomass.

Energy Expenditure Equations

To account for energy expended by swimming and via respiration, I used equations for the swimming costs of salmon taken from Harvey and Railsback (2009). These equations were a function of water temperature, dissolved oxygen, and water velocity. They account for both the calories burned when a fish is at rest by basic metabolism and the calories burned while foraging.

Quantification of Fish Behavior

We used a GoPro camera to take video samples of the pools, which allowed us to quantify the number of behaviors observed (behaviors included drift foraging, search foraging, attacks, and movement) on an individual fish basis. We analyzed six randomly selected 30 second intervals from each video, then categorized and counted each activity exhibited by each fish every three seconds (repeated 10 times, to reach the full 30 seconds). We summed all of the total observed behaviors for each date, then separated the behaviors and summarized by date and by pool.

RESULTS

Bioenergetics of Drift Foraging: Overall, drift foraging was energetically beneficial in Early-to-mid May, but in late May, the Net Rate of Energy Intake (NREI) in all three of the streams dropped to become negative (Figure 2). The energetic profitabilities eventually levelled off at slightly above -0.02 Joules per second. Our laboratory team was not able to process the early May sample for pool 18.4, due to the COVID-19 pandemic limiting our access to the laboratory.

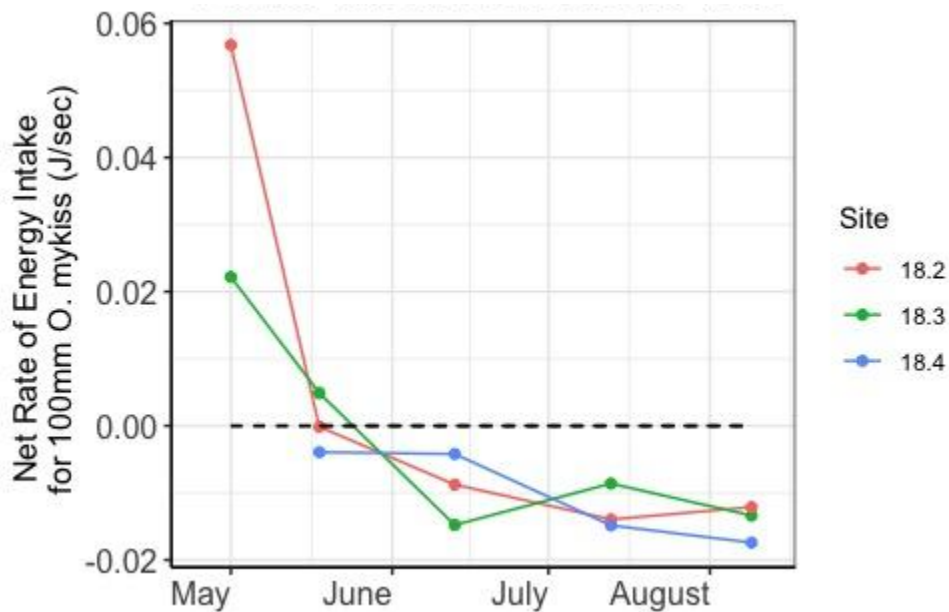


Figure 2: The net rate of energy intake for drift foraging.

Bioenergetics of Search Foraging: The energetic profitability of search foraging started off as negative at the beginning of the summer, and then increased for two of the pools to significantly above zero from late May to late July, however did not change over time for pool 18.4 (Figure 3), remaining negative the entire time. The energy intake of search foraging was dependent on the benthic flux, the flux of the drift that was not eaten at the front of the pool, and the surface flux of macroinvertebrates.

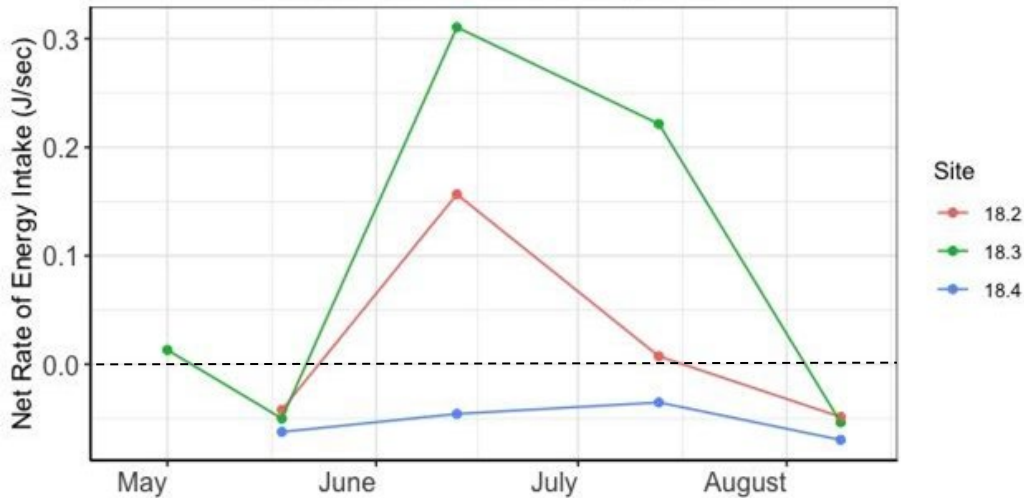


Figure 3: The net rate of energy intake for search foraging.

Fish Foraging Behavior

The percent of observed drift foraging behaviors decreased in each pool throughout the summer, while the percentage of search foraging behavior increased (Figure 4). Non-foraging behavior (including movement and aggression) increased significantly in each pool, reaching 100% of the observed behaviors in pool 18.4 and at least 75% of the observed behaviors in the other two pools. The percent of observed behavior that is search foraging can be predicted accurately by measurements of the NREI of search foraging, but not by the velocity at the head of the pool (Table 1).

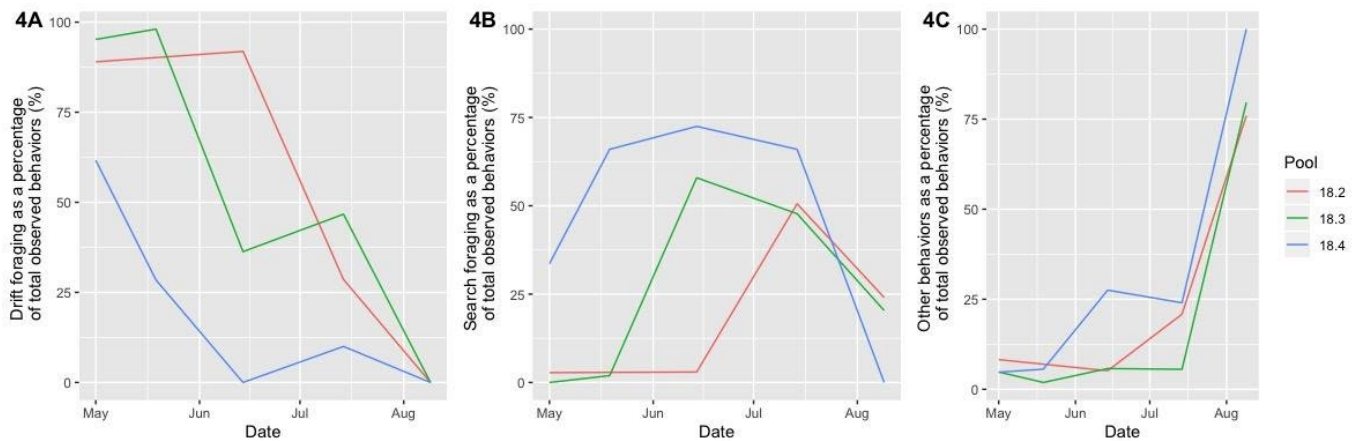


Figure 4: Percentages of foraging behavior observed. The tallied behaviors for each sampling date were calculated, and then (a) drift foraging, (b) search foraging, and (c) other behaviors (such as aggression and movement independent of obtaining food) were calculated as a percentage of the total observed behaviors.

Table 1: Two-Way ANOVA to predict percent search foraging based on velocity and NREI of search foraging. Search Foraging can not be estimated based on the velocity at the head of the pool, but the NREI of Search foraging has a significant p-value of 0.0169.

	df	Sum Sq.	Mean Square	F Value	P-value
Velocity	1	925	925	1.973	0.1937
NREI of search foraging	1	4010	4010	8.559	0.0169
Residuals	9	4217	469	NA	NA

DISCUSSION

The percent of search foraging observed throughout the summer can be predicted by the NREI of search foraging, which suggests that juvenile salmonids determine their mode of foraging based on the relative net energy intake of each foraging mode. The velocity of water did not significantly predict the percentage of search foraging (Table 1), which aligns with previous studies that found search foraging to be independent of water velocity (Harvey & Railsback 2011). Drift foraging started out as the most observed behavior in all pools in the early summer, and then decreased to 0% in August (Figure 4) due to no flow coming into any of the pools. In the mid-summer months of June and July, it was energetically favorable to search forage in pools 18.2 and 18.3, but the NREI of search foraging for pool 18.4 remained negative for the entire summer (Figure 3), which implies that particular characteristics about the pools make them favorable for certain modes of foraging at certain times. On an individual basis, the fish were able to determine which foraging technique was beneficial based on the habitat characteristics they observed from their direct environment, which has significant potential to link habitat characteristics to the population dynamics of the fish – a necessary component for salmonid conservation (Harvey & Railsback 2014).

The results indicate that if a fish were to maximize its net energy intake throughout the entire summer months, then it would need to drift forage in spring and early summer (Figure 2), and then switch to search foraging starting in late-May/early-June (Figure 3). Most bioenergetics models do not take into account this energetically beneficial search foraging option, thereby

assuming that the fish would be drift-feeding year-round, even when there is no drift to feed on! These models, when implemented in any stream within a Mediterranean climate, would fail to link the habitat conditions to the fish population dynamics, and therefore would not be able to account for phenology. There have also been observations of fish obtaining at least a portion of their diet from the stream benthos during high velocity stream conditions (Tippets & Moyle 1978, Grant & Noakes 1987), which prompts research into whether the assumption that drift foraging is the most efficient foraging strategy in every part of the high velocity stream habitat is valid.

Maximizing NREI

It is important to emphasize that the fish are assessing the *relative* NREI of each foraging mode (Nielson 1992). Even in some instances, in which the NREI of search foraging is negative, it still might be *less* negative than the NREI of drift foraging, which might translate to fewer calories lost overall. A fundamental assumption of bioenergetics models is that fish are able to detect the relative energetic gain of each foraging mode to a certain extent (Fausch 1984), and the results from this paper show that they will switch to the more positive NREI foraging mode, so the fish have the capacity to alter their behavior in response to external environmental variables. The swimming costs of drift foraging are well-established, because drift is assumed to be the most efficient foraging method for stream-dwelling fish (Naman et al. 2018). However, when the drift flux is very small later in the season, as shown in Porter Creek, that represents a negative NREI for that foraging mode, which translates to decreased growth and even death in some fish. The benthic and surface fluxes are still available though during the times of low flow (Figures 2 and 3) since they are primarily independent of stream flow, so depending on the energetic costs of search foraging, it could be worth it. Also, dissolved oxygen decreased and temperature increased in each pool as the summer progressed, which means that the fish had a higher metabolism rate and therefore burned more calories while foraging and at rest (Railsback & Harvey 2009), making maximizing their NREI even more important.

Individual-Based Models

Fish will readily shift foraging tactics in response to changes in the magnitude and distributions of food (Grant & Noakes 1987), but in this experiment, the changes in food availability directly correspond to changes in the fish's physical environment – the flow of the stream. This feature of the habitat is why Individual-Based Models (IBMs) are important: they allow one to link the habitat conditions to fish population dynamics, because instead of imposing a certain type of behavior on a population, IBMs make the assumption that each individual fish will make certain decisions to reach certain objectives (in this case, maximizing NREI) (Railsback & Harvey 2001). The fish base their energetic decisions based on (1) the amount of potential calories from each macroinvertebrate flux, and (2) the calories that they would expend while foraging for each macroinvertebrate flux. Since respiration is more energetically taxing for the fish in higher temperatures and lower dissolved oxygen conditions (Giller & Malmqvist 1999), the abiotic habitat conditions do influence the fish's behavior. These IBMs are beneficial for predicting the direct responses of populations in response to alterations of specific habitat variables, as well as the cumulative ecosystem responses (Harvey & Railsback 2014).

Limitations and Future Directions

In this study, I had to make some assumptions, but I attempted to preserve the relationships and behaviors that were observed in previous papers as best I could. I had to assume that the fish were able to accurately determine which of the fluxes represented the largest net energy gain to themselves. Previous papers have established that fish are able to sense stream velocity conditions at different areas of the pool (Gowan et al. 2007), and that was the primary physical cue that they used to decide where and how to forage, but there are other factors at play, which are less understood. Overall though, when velocities are sufficiently high to allow drift foraging, I assumed that the fish would choose that method, but more analysis is needed to determine what other variables are at play in the late summer low flow conditions. Also, this model doesn't take intraspecific or interspecific competition into account, which could confound the results a little bit, since there were other non-salmonid fish in the pools, such as sculpin, California roach, and pikeminnow. The differing abundances of other fish species could have mildly adjusted the biomass results, but I made the assumption that it affected each of the three macroinvertebrate

fluxes equally, so it wouldn't matter when assessing relative energetic benefit. I am not sure how valid this assumption is, so further research into that topic is necessary.

This experimental design needs to be replicated multiple times in other mediterranean streams in order to test the validity of the assumptions that my model made. Drift foraging is primarily used as the sole measurement of energetic efficiency in higher order aquatic food webs, so these future experiments will need to coordinate and standardize the methods for evaluating both benthic and surface fluxes in streams. Including these alternative foraging methods is essential in determining how the fish relate to the environment, which is necessary for their conservation. Incorporating these assumptions into pre-existing models also allows more thorough testing of ecological theories, such as optimal foraging theory, competition (both interspecific and intraspecific), and size-based dominance hierarchies used by salmonids.

CONCLUSION

California stream management occurs primarily on a regional scale, so a lot of customization of these models will be required to successfully implement bioenergetics models into specific stream management regimes. The most important aspects of these salmonid bioenergetics models is that they accurately relate the habitat conditions to the fish population dynamics. Bioenergetics models that only include drift foraging are not representative of the Mediterranean hydrologically dynamic streams of California's central coast, as shown by this paper, so search foraging is an essential component of these models. The incorporation of additional foraging modes into pre-existing bioenergetics models allows managers of these streams to consider streamflow and fish bioenergetic statuses in their management decisions. With an increased ability to predict fish growth using calories, we are one step closer to determining the ways that fish and other aquatic animals relate to their environments and to each other. Determining this relationship is essential for the conservation of these endangered and threatened fish species, and with the implementation of more accurate bioenergetics models, managing entities are able to more accurately preserve and restore these relationships.

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