1. Project Title Page

a. Project Title

Linking fish foraging with population dynamics: Incorporating variable consumption into the Stream Salmonid Simulator

b. Date of Proposal

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2. Project Description

a. Priority Item

Topic 2: Development of a foodscape model for incorporation into the Stream Salmonid Simulator

b. Project Intention and Significance.

The intent of this project is to improve the population-level fish modelling capacity in the Trinity River by expanding the Stream Salmonid Simulator (S3) model to: 1) allow juvenile Chinook Salmon consumption to vary across spatial-temporal dimensions, and 2) use a mechanistic drift-foraging model to estimate S3 consumption inputs from information on macroinvertebrate drift. This improved modelling capacity will leverage completed (King 2024, Starkey-Owens 2020, Williamshen et al. 2023) and ongoing field research on macroinvertebrate drift composition and concentration to link management actions to juvenile fish growth and survival. This modelling capacity would allow future investigations to link flow management scenarios that may alter drift food availability with consumption and population-level metrics provided by S3.

c. Project Goals, Objectives, and Adaptive Management

This project furthers the fundamental goal of the TRRP to restore and sustain natural production of anadromous fish populations in the Trinity River to pre-dam levels. Specifically, this project will address two key uncertainties described in the TRRP Science Plan (Pickard et al. 2023): nutrient flux (key science plan uncertainty 2) and fish production (key science plan uncertainty 4). Allowing consumption to vary in S3 related to drift food availability will improve our understanding of how management actions like dam discharge scheduling affect energy transfer through trophic levels to juvenile fish (nutrient flux). For instance, alternative flow regimes can alter both the physical habitat (water depths, velocities, and temperatures) and food availability (via both altered water velocities influencing delivery rates and potentially through flow-invertebrate drift relationships) on which juvenile Chinook Salmon rely. When mechanistic drift-foraging models are applied alongside hydrodynamic models, they provide a linkage between flow management actions which alter the physical habitat and food availability, and biological responses, such as fish consumption or growth potential. This added capability will also allow us to better understand whether drift food availability is a bottleneck to fish production at the juvenile rearing life stage (fish production). Reducing these key uncertainties will inform adaptive management and lead to progress in meeting TRRP objectives (TRRP 2024). Improved understanding of the relationship between flow, drift food availability, and consumption by fish will provide more realistic expectations of how linking phenology of prey species and fish species (Fish 9) will increase our ability to achieve adult fish production (Fish 1-4).

d. Methods

Task 1: Incorporating spatiotemporal consumption rates into S3:

S3's spatiotemporal resolution allows demographic parameters such as movement and survival to vary in response to the daily environmental conditions within each of the model's mesohabitat units. However, while growth rate in S3 varies spatiotemporally in response to daily water temperature, to date, S3 has assumed that fish consumption is constant. The current version of S3 employs the Wisconsin bioenergetics model (Stewart and Ibarra 1991; Plumb and Moffitt 2015), which allows for a variable consumption rate, expressed as the proportion of maximum daily consumption (pCmax). Currently, this proportion has been assumed constant at a value of two-thirds based on the literature (Armstrong and Schindler 2011, see appendix), and comparison between the Ratkowsky model (Perry et al. 2015) and Wisconsin model (see Figure 9, Perry et al. 2018).

We propose extending S3 to allow for consumption to vary both spatially (at the mesohabitat scale) and temporally (at a daily time step). This extension would allow S3 to represent a broader set of ecological dynamics and make the model sensitive to management scenarios that affect food availability. For example, winter flows (Winter Flow Project) are hypothesized to alter food availability through colonization of newly inundated habitat by macroinvertebrates (Abel et al. 2022), which may influence consumption rates. This task involves structuring S3 to accept an $h \times t$ matrix of pCmax as model input (h = number of habitat units, t = number of days), instead of a single value. In addition, we will review the current version of the Wisconsin bioenergetics model used in S3 to ensure accuracy of the parameter set used and compatibility with estimates of consumption from Task 2.

Task 2: Translating macroinvertebrate drift into fish consumption for S3

Providing functionality for pCmax to vary is requisite for understanding how variation in consumption affects population dynamics, but TRRP partners need to translate hypotheses about macroinvertebrate drift into consumption rates for juvenile Chinook Salmon. For example, if macroinvertebrate colonization of inundated habitat results in a subsequent increase in drift concentration, how does this increase in drift affect maximum daily consumption? To answer such questions, we propose to inform consumption estimates used as input to S3 by applying a drift-foraging model based on Naman et al. (2020).

Although drift-foraging models were developed to estimate Net Rate of Energy Intake (NREI) and calculate bioenergetics-based habitat suitability criteria, these models can also be used to estimate the proportion of maximum daily consumption. Drift-foraging models estimate the benefits and costs of maintaining feeding station at a particular depth, water velocity, and water temperature given the characteristics of macroinvertebrate drift available to fish of a given size (Figure 1). Maximum daily consumption varies in relation to all these inputs based on the relationships that define the mechanistic foraging or bioenergetics model. For example, while Figure 1 illustrates variation in pCmax due to fish size (x-axis) and water velocity (colors), pCmax will also vary as a function of water depth (held constant in Figure 1), and decrease in very shallow water as the foraging area is truncated at the surface. Similarly, attributes of the invertebrate drift, such as concentration, composition, and size distribution, may influence consumption and subsequent estimates of growth potential (see Dodrill et al. 2016).

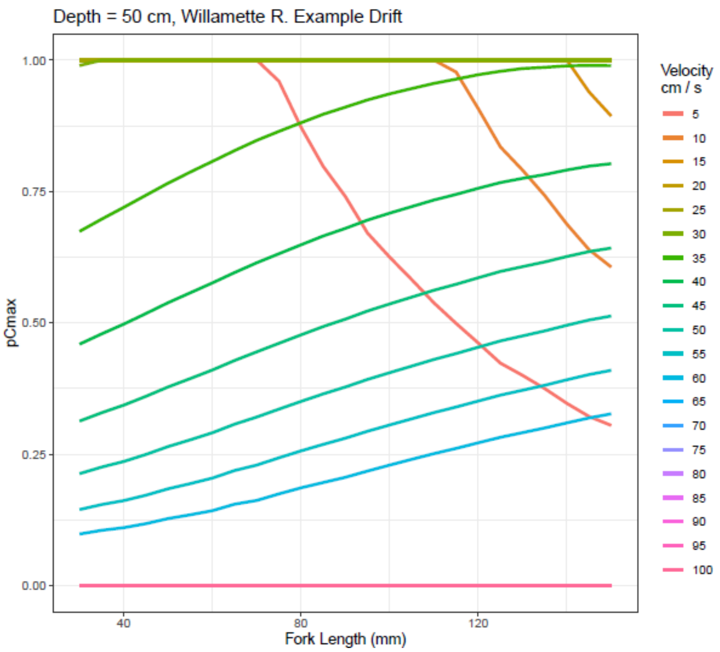

Figure 1. pCmax as a function of Chinook Salmon fork length predicted by the Naman et al. (2020) drift foraging model over a range of velocities based on a flow depth of 50cm and using drift data from an ongoing USGS study in the Willamette River, OR.

To apply this modelling technique, we propose to use an existing 2D hydrodynamic model of the 40-mile restoration reach (SRH-2D, Bradley 2016). The spatial resolution of the SRH-2D model near the channel margins is typically 2 ft. by 10 ft, and the full model domain is composed of more than two million cells. Water depth and velocity are simulated within each cell, providing the hydrodynamic information needed to apply a spatially explicit drift-foraging model over a range of river flows. The full SRH-2D model domain will likely be reduced when applying the drift-foraging model, including only wetted cells for a given flow scenario, and excluding high depth and velocity areas unlikely to represent juvenile Chinook foraging habitat. The studies of Starkey-Owens (2020) and Williamshen (2023) will provide a baseline characterization of invertebrate drift. This would ideally include key information on the concentration (number / volume), size distribution, and taxonomic composition of the drift. While these studies do provide baseline information, considerable uncertainty still exists for characterizing spatiotemporal variation in the Trinity River and how invertebrate drift may respond to alternative management scenarios.

To construct updated inputs required for S3, the drift-foraging model will predict pCmax for each cell in the 2D hydrodynamic model, which can then be summarized over cells that fall within each of S3's coarser-scale mesohabitat units. After examining the distribution of pCmax within a series of mesohabitat units, an appropriate summary metric will be chosen. This approach is analogous to the procedure used to estimate carrying capacity inputs for S3 but will be much more computationally intensive. For carrying capacity, we apply the abundance model of Som et al. (2017) to each cell of SRH-2D and summarize the total capacity over the cells of each S3 mesohabitat unit for model runs of SRH-2D at 16 different river flows. This data set provides the inputs to S3 where a pre-processing function maps capacity to the timeseries of daily river flow by linearly interpolating between flows modeled in SRH-2D.

We will apply this same framework to pCmax, but several more dimensions of inputs are required because pCmax depends not only on river depths and velocities, but also on water temperature, fish size, and characteristics of the drift (primarily concentration, but also potentially composition and size distribution). For each modeled river discharge, we will apply the drift-foraging model over a range of fish size, water temperature, and invertebrate drift. This data set will be provided as input to S3, allowing the user to specify drift information at update locations along the length of the model domain. We will develop a multidimensional interpolation routine that will use the "lookup table" of pCmax produced by the drift-foraging model to interpolate pCmax given the flow, temperature, drift, and fish size on a given day, in a given habitat unit. This modeling will be computationally intensive. For example, if we run the drift-foraging model for 20 levels each of fish size, water temperature, and drift concentration, that works out to 8,000 runs of the drift-foraging model applied to a portion of the two million SRH-2D model cells at a single river discharge. Therefore, we will make use of USGS's High Performance Computing Center to take advantage of thousands of CPUs for parallel processing. In the application of this approach, simplifications to the various dimensions may be necessary to reduce this complexity, while preserving essential ecological or physical components. For instance, the full SRH-2D model domain consists of several million individual cells and may be simplified by clipping any high velocity and deep cells, instead focusing on the channel margins known to have higher habitat use by foraging juvenile Chinook Salmon. Similarly, an approach where characteristic channel units (e.g. pools, riffles, runs) are modelled and extrapolated to similar unmodelled locations may be used to simplify the necessary computations.

Task 3: Evaluating pCmax in updated S3 model

Estimates of consumption from the drift-foraging model represent the potential of a given SRH-2D cell to support foraging and growth. An open question in the application of these methods is how this potential is realized when considering other ecological factors such as fish densities, competition, and predation risk. In addition, when drift-foraging models are used to estimate bioenergetics-based habitat suitability criteria, estimates of NREI are relativized, often scaling between 0 and 1, and interpreted as higher values representing more quality habitat (Naman et al. 2020). For our application, the absolute values of NREI are meaningful and daily consumption is capped at the physiological maximum, potentially leading to an overprediction of growth potential. For these reasons, we propose a comparison between a baseline represented by the current assumption of constant pCmax in S3, and two different approaches to generate consumption estimates.

The first approach we propose will use the drift-foraging model outlined in Task 2 to estimate pCmax, given assumptions of how invertebrate drift may vary both spatially and temporally in the Trinity River. This will use any current and completed investigations that characterize invertebrate drift as a starting point (i.e. Starkey-Owens 2020, and Williamshen et al. 2023). Given that the studies, of Starkey-Owens (2020) and Williamshen et al. (2023), only provide a snapshot of invertebrate drift at a limited set of locations and time periods, we propose working with TRRP partners to develop a realistic scenario that represents the current understanding of how drift may vary over space and time across the S3 model domain.

In the second approach, we propose to directly estimate pCmax from *in situ* growth rates of a limited collection of up to 250 juvenile Chinook Salmon. Given the logistics of estimating growth from tagging studies, we propose collecting otoliths and analyzing daily increments from fish collected within the restoration reach. To estimate pCmax from daily otolith increments, we propose a bioenergetics-based approach which will account for the temperature history of fish at a given location. Statistical models of fish growth based on bioenergetics (Walters and Essington 2010) have recently been fit to otolith increment data (Essington et al. 2022). Due to the parametrization of these models and the incorporation of functional forms defining how parameters vary with temperature, these methods can separate the effects of temperature from energetic intake and loss terms. Empirical estimates of pCmax will also be useful in comparison to the drift-foraging model to better understand whether the model produces realistic estimates of pCmax. Fish sampling will occur in 2026 from approximately February until June at two-week intervals at each of three sites spanning the 40-mile restoration reach using seines to capture fish. This sampling regime will target locally rearing fish (as opposed to actively migrating fish encountered at screw traps) with high temporal frequency so that recent growth (weeks prior to capture) can be analyzed. To complete this task, we will work with TRRP partners to collect juvenile Chinook Salmon. Otoliths will be extracted, processed, and analyzed by the USGS's scale and otolith lab at the Western Fisheries Research Center or an equivalent lab (university or private).

Once pCmax estimates are available from both approaches, we will run S3 for historical water years and compare observed fish size at the Pear Tree trap with predicted fish sizes. We can then evaluate whether the updated models improve goodness of fit to observed data relative to the baseline model that uses a constant pCmax set to 0.66. This exercise will help guide further information needs and formalize hypotheses related to how fish consumption and food availability may vary across space and time in the Trinity River.

Task 4: Reporting

The project will be primarily managed by USGS staff in collaboration with other PIs. Reporting will occur in stages, associated with Tasks 1 – 3 (see Project Timeline). Briefly, an updated S3 R package reflecting work under Task 1 will be completed by end of federal fiscal year (FY) 2026, with modifications associated with Task 2 completed by end of FY 2027. These R package updates include documentation associated with the expanded model capability. A peer reviewed report or manuscript will summarize project Tasks and will be submitted by the end of FY 2027.

Strengths, Weaknesses, and Challenges

Parameterizing the drift-foraging model at sufficient spatial-temporal scales, bridging the gap between SRH-2D cells and larger spatial units (mesohabitat or reaches), and interpreting the drift-foraging based consumption estimates represents several major challenges:

- While the approach outlined in Task 1 will allow for fine scale variation (both temporal and spatial) in consumption and drift, this structure allows significant flexibility for how inputs are specified. For example, to represent seasonal shifts in invertebrate production and delivery, consumption could vary by month (assumed constant within a month), or consumption could be constant across mesohabitat units comprising larger sections of the Trinity River. Additionally, this expanded S3 functionality will allow TRRP to formalize hypotheses about how invertebrate drift may vary in relation to alternative management scenarios and evaluate population level responses. In absence of an invertebrate drift models which predict drift concentration temporally, spatially, or in response to a flow-invertebrate drift relationship, these hypotheses may be formulated qualitatively (i.e., what if the management action alters drift by X %, what would the potential population level response in juvenile Chinook Salmon be?). This functionality represents a major strength and allows S3 to be parameterized in more complex ways as other modelling tools, data, and understanding of ecological dynamics progress in the Trinity River.
- The drift-foraging model estimates of consumption represent the potential for a given location (SRH-2D cell) to support foraging and growth. However, the extent to which this potential is realized, given ecological factors such as competition and predation, in applied settings is uncertain. Summarizing the fine scale (SRH-2D cells) potential consumption estimates to larger spatial units will likely require acknowledging these additional ecological factors and dynamics to some extent.
- Task 2 represents significant computational burden, which may be partially addressed using high-performance computing and parallelization. Simplification in the hydrologic modelling domain or other facets of the project may be required if the process is too computationally burdensome. Collaboration with TRRP workgroups will inform these decisions.
- Fully evaluating hypotheses related to altered flows and ecological responses (i.e., Winter Flow Project), may require methods that link benthic invertebrate densities with drift concentrations in a mechanistic fashion such as a drift transport model (Hayes et al. 2007; Hayes et al. 2019; Anderson et al. 2013). Alternatively, paired sampling of benthic invertebrates and drift across a range of flow conditions could be used to build empirical relationships between benthic densities, river flow and drift concentration (Kennedy et al. 2014). Although we don't anticipate developing this capacity within this project, the avenues could be useful extensions to the modeling proposed here.
- Estimating juvenile Chinook Salmon growth rates from otoliths will require some assumptions regarding the conditions (habitats, temperature regimes) under which the growth occurred. The sampling frequency (two-week intervals) and analysis of only recent growth (daily increments from the previous weeks before capture) will help to

bound the potential growth conditions. Inferences may be limited to the observed temperatures during the 2026 sampling season and to the locations in which fish are collected. Sampling years with more variation in temperatures would allow for modelling across a larger range of temperatures, however, this is beyond the scope and timeline of the current proposal. If growth information derived from otoliths does prove to be useful for direct assessment of management actions, the program may consider implementing standardized fish collections across time and space.

- The drift-foraging model proposed for use in Task 2 estimates consumption rate per second, which needs to be translated to a daily rate expressed as pCmax for incorporation into S3. There is a risk of overestimating pCmax when expanding the consumption rate per second given foraging during daylight hours. One potential solution to address this issue is to incorporate a digestion processing sub-routine into the drift-foraging model. While significant drift-foraging model development is outside the scope of the current proposal, we may implement this sub-routine to address overprediction of pCmax in Task 2.
- Applying the Naman et al. (2020) drift-foraging model requires numerous assumptions, such as the type of foraging (surface vs. water column), depth of fish foraging, hours of foraging time, ect. The studies of Williamshen et al. (2023) and Starkey-Owens (2020) used drift nets to sample both water column and surface drift, however the proposed drift-foraging model only considers water column foraging, which may introduce some errors in the estimates of consumption rates. Clearly defining the model assumptions and acknowledging the implications of these assumptions will be required given the focus of this proposal. While development of new drift-foraging methods is beyond the scope of this proposal, we will collaborate with TRRP science advisors and staff to make assumptions that best represent conditions in the Trinity River.
- This proposal does not include any additional drift collections, primarily due to the expense and time associated with sample processing. This may limit some inferences, especially related to the analysis of observed growth from otoliths and our ability to directly compare estimates of consumption from the drift-foraging model with estimates from the statistical growth (otolith) model.

e. Product Timeline

Analysis and reporting will be primarily the responsibility of USGS staff in consultation with other PIs following the timeline below:

- An updated S3 R package that reflects changes described in Task 1 will be provided by end of FY 2026. Any additional information pertinent to Task 2 (i.e., multidimensional interpolation routine) will be provided as a S3 R package update by end of FY 2027.
- Collection and processing of juvenile Chinook Salmon otoliths will be completed in FY 2026.

- A final data set, including comprehensive metadata, will be provided in a commonly used format (e.g., MS Access, Excel, or equivalent) by end of FY 2027. This dataset will include otolith data associated with Task 3.
- A draft report for peer review, or journal manuscript, documenting the proposed work will be submitted for review by the end of FY 2027.
- Final report or journal paper will follow the completion of peer review process within 12 months.

3. Budget

The total budget for this proposal is $336,266 with additional in-kind contributions by non-USGS partners. The project is intended to be complete in FY 2026 and FY 2027 with the full amount requested in FY 2026. Additional details are provided in the attached budget spreadsheet “USGS AFA Tasks Workbook_FY2026.xlsx”

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