


FEATURE


Bioenergetic Habitat Suitability Curves for Instream Flow Modeling:



Introducing User-Friendly Software and its Potential Applications

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Habitat suitability curves (HSCs) are the biological component of habitat simulation tools used to evaluate instream flow management trade-offs (e.g., the physical habitat simulation model). However, traditional HSCs based on empirical observations of habitat use relative to availability have been criticized for generating biased estimates of flow requirements and for being poorly transferable across locations. For fish like salmonids that feed on drifting invertebrates, bioenergetics-based foraging models that relate habitat conditions to net energy gain offer an alternative approach that addresses some of these shortcomings. To make this technique more accessible for practitioners, we present free and user-friendly software for generating bioenergetics-based HSCs. The software also allows sensitivity analyses of HSCs to factors like fish size or prey abundance as well as direct integration of hydraulic data. While some caveats remain, bioenergetic HSCs should offer a more rigorous and credible means for quantifying habitat suitability for instream flow modeling.

INTRODUCTION

Streams and rivers provide habitat for many culturally and economically important fish species as well as water to support industry and basic societal needs. When these two functions conflict, difficult management trade-offs can arise between maintaining flows to support viable fish populations and allocating water for human use. A wide array of techniques have been developed to inform these management decisions, which critically depend on credible predictions of how fish will respond to flow changes (Lamouroux et al. 2017). One of the most widely used of these methods is the physical habitat simulation model (PHABSIM; Bovee et al. 1998), which links a physical model predicting how hydraulic conditions like depth and velocity change with flow to a biological model that describes the suitability of those hydraulic conditions for a target species.

The popularity of PHABSIM undoubtedly relates to its conceptual and computational simplicity. In particular, the biological component of PHABSIM is premised on the ecologically intuitive notion that habitat conditions are more suitable where fish most frequently occur. Specifically, the biological model in PHABSIM is represented by habitat suitability curves (HSCs), standardized univariate habitat selection indices for variables, such as depth, velocity, and substrate, that are straightforward to generate empirically from observations of habitat use or to obtain from existing literature or expert opinion. This approach is widely used, but has important limitations that have been the basis of frequent criticism (Mathur et al. 1985; Orth 1987; Lancaster and Downes 2010). A particularly strong concern is that observed habitat use can be an unreliable indicator of habitat quality (Van Horne 1983), especially for territorial fishes like salmonids, where subordinates are often displaced into lower-quality habitats at high densities (Nakano 1995). As a result, flow requirements based on HSCs can be significantly biased (Beecher et al. 2010; Hayes et al. 2016). In addition, HSCs have limited transferability across locations due to their sensitivity to environmental variables, such as temperature and food abundance (Rosenfeld et al. 2005).

Recognizing the biases in HSCs, instream flow science has made considerable advances towards more dynamic approaches to instream flow management (Anderson et al. 2006; Yarnell et al. 2015). These include more mechanistic habitat suitability models rooted in fundamental animal physiology or behavior, which link flow and habitat conditions to more direct correlates of fitness (Anderson et al. 2006; Railsback 2016). However, despite their advantages, mechanistic habitat suitability models have gained limited traction with instream flow practitioners, likely due to the complexity of model development and the relatively large amount of information required for calibration (Reiser and Hilgert 2018). Consequently, HSCs within the PHABSIM framework remain widely used in

practice and will likely remain so until flow management transitions to these emerging approaches.

Instream flow assessments often focus on salmonids in areas where they are present, given their high societal value and wide range. For these taxa, as well as other fishes that feed on drifting invertebrates, bioenergetics-based foraging models have emerged as an increasingly tractable mechanistic approach for stream habitat evaluation (Urabe et al. 2010; Rosenfeld et al. 2014; Wall et al. 2016). Drift-foraging models describe how habitat conditions influence a fish's energy balance while it feeds in flowing water (Box 1), ultimately predicting the net rate of energy intake (NREI; energy gains minus losses) that a fish would experience for a given depth and velocity. The NREI provides a tractable and biologically relevant currency of habitat suitability, which can replace or complement traditional HSCs within the PHABSIM

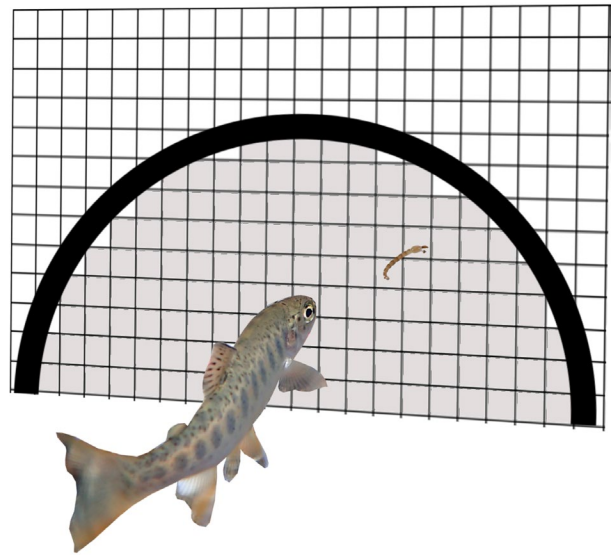


Figure 1. Conceptual schematic of the cross-sectional area of a drift-feeding fish. The black semi-circle represents the reaction distance, where a fish can detect drifting prey. Net rate of energy intake calculations are made in a series of rectangular grid cells within this volume, which are laterally symmetric around the focal point. The boundary of the reaction area is defined based on whether the center of grid cells fall within the reaction distance (grey shaded cells in figure). This creates a pixilated rather than perfectly hemispherical boundary, which differs from previous drift-foraging model implementations. However, grid cell size is customizable, so users can approximate a hemispherical boundary by using a smaller grid size. The effective area within this grid where a fish can capture drifting prey is defined by a capture success function, where capture probability declines with water velocity and distance from the focal point.

Box 1. A brief primer on drift-foraging bioenergetics models.

Drift-foraging models describe how habitat conditions (e.g., depth, velocity, prey abundance) influence a fish's energy balance while it feeds on drifting invertebrates in flowing water. The majority of these models have been developed for salmonids, but they could also be applied to other drift-feeders assuming relative habitat suitability is of interest (as opposed to absolute net rate of energy intake [NREI], which will be sensitive to species-specific swimming cost and energy intake parameters; Hill and Grossman 1993; Grossman 2014). Here, we provide a brief overview of the modeling process and refer readers seeking more details to the foundational literature (Fausch 1984; Hughes and Dill 1990; Hughes et al. 2003; Hayes et al. 2007) or to recent reviews (Piccolo et al. 2014; Rosenfeld et al. 2014).

Drift-foraging models estimate the potential NREI (usually expressed as joules per second) that a fish could achieve while drift feeding at a given depth and velocity. NREI is computed as the difference between the total energy a fish could acquire from feeding (gross rate of energy intake; GREI) minus the energetic costs (EC) it would incur from swimming, maneuvering to capture prey, and digestive metabolism (energy costs) This is defined as follows:

$$\text{NREI} = \text{GREI} - \text{EC}$$

The defining optimization process in drift-foraging models is the trade-off between increasing drift flux but declining capture success and greater swimming costs as velocity increases. The basic modeling approach consists of several components. First, the volume of water a fish can scan is determined based on the distance at which a fish can detect prey of different sizes (Hughes and Dill 1990). This volume is then subdivided into discrete cells adjacent to the fish (Figure 1), and energy intake is computed as the volume of water passing through each cell multiplied by the concentration of prey and by a capture success function that defines the likelihood that a given prey item will be intercepted (Hill and Grossman 1993; Rosenfeld et al. 2014).

Energy costs, the other main model component, are divided into costs associated with swimming at the focal point and costs associated with maneuvering to intercept prey. Both of these components draw from physiological studies (Hughes and Kelly 1996; reviewed in Trudel and Welch 2005) and are related to velocity, fish size, and temperature. Energy costs due to digestive metabolism are expressed as constants that scale energy gain to account for losses due to metabolic processes (e.g., egestion and excretion) or, alternatively, as temperature- and size-dependent functions based on Wisconsin bioenergetic models (Hanson 1997).

Other factors can be added to drift-foraging models to modify energy intake or expenditure functions. For example, turbidity can be accounted for by adding a function that reduces a fish's reaction volume (i.e., to account for prey being less visible in more turbid water). Similarly, the effects of turbulence can be included as a modification to swimming cost functions to account for the complex hydraulic environment in natural rivers (Enders et al. 2003).

Drift-foraging models have been shown to effectively rank habitat quality, as evidenced by their ability to predict habitat selection (Hughes et al. 2003), density (Urabe et al. 2010), and relative growth rates (Naman et al. 2019). However, it is important to recognize that there is still uncertainty in numerous drift-foraging model components (Rosenfeld et al. 2014). We describe this uncertainty, and how best to deal with it, in detail in the user manual accompanying the software.

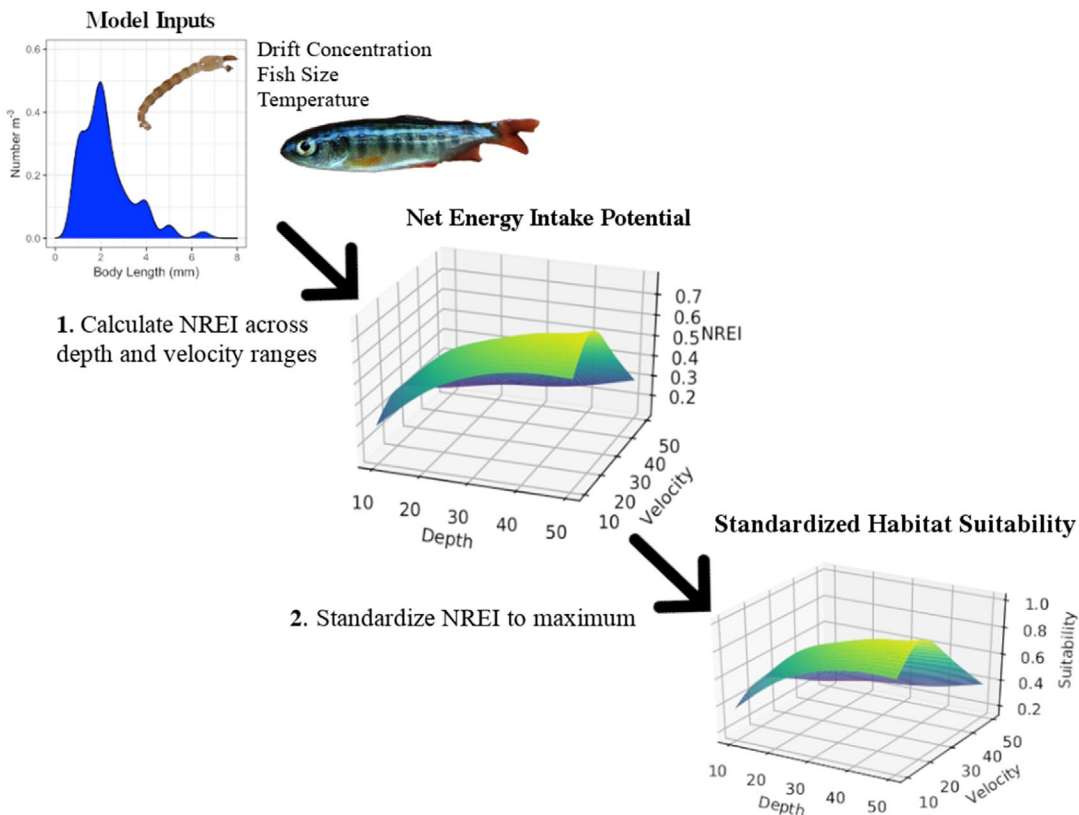


Figure 2. Conceptual overview of procedure for computing bioenergetic habitat suitability curves. First the initial variables are parameterized; these include fish size, concentration and size distribution of invertebrate drift, and temperature (other specifications are discussed in the manual). The model then computes net energy intake rate (NREI) across all possible discrete combinations of depth and velocity over ranges specified by the user, which results in a bivariate NREI surface (step 1). This surface is then standardized to a maximum of 1 by dividing all values by the maximum NREI value (step 2). This standardized bioenergetic suitability surface (bioenergetic HSC) can then be combined with hydraulic data in the same manner as traditional HSCs within PHABSIM.

framework (Baker and Coon 1997; Rosenfeld et al. 2016), essentially acting as an intermediate step between traditional HSCs (hereafter “frequency-based HSCs”) and more complex mechanistic models.

While bioenergetic HSCs based on drift-foraging models are more straightforward to compute and require less information than more detailed mechanistic approaches (e.g., spatially explicit or individual-based models), they still involve some complex calculations, which is a barrier to their general application. To address this issue, we present BioenergeticHSC, a free and user-friendly modeling software designed to make bioenergetic HSCs widely accessible to instream flow practitioners. Here, we provide a conceptual overview of the modeling approach, describe the specific functionality of the software, and discuss its advantages, caveats, and potential applications.

OVERVIEW OF MODELING PROCEDURE AND SOFTWARE

Bioenergetic HSCs are based on a drift-foraging bioenergetics model, which predicts NREI for drift-feeding fish at discrete combinations of depth and velocity. To generate bioenergetics-based HSCs, NREI (J/s) is calculated (Box 1) across all combinations of user-specified ranges of depth and velocity, then NREI is standardized to a maximum of 1 by dividing each value by the overall maximum across all depth and velocity combinations (Figure 2). The resulting standardized curve (or response surface) can then be combined with habitat values just like traditional HSCs within the PHABSIM framework.

BioenergeticHSC software is designed to be a user-friendly tool for rapidly generating bioenergetic HSCs and can be downloaded for free at <https://bit.ly/324ktvm>. It is based on a menu-driven graphical user interface environment (Figure 3), where users can specify biotic and abiotic input variables (e.g., fish size,

temperature) and model attributes (e.g., swimming cost functions, turbidity, and turbulence adjustments). A comprehensive manual accompanying the software explains each component in detail, provides guidelines on best practices, and describes the underlying assumptions and limitations; the manual is included in the software download or can be found at <https://bit.ly/324ktvm>. While the software requires no prior programming knowledge, we have made the source Python code available so that users have the option to create modifications, report bugs, or incorporate the program into larger modules.

The only external data required to generate standardized bioenergetic HSCs are concentrations (number/m³) of different size-classes of drifting invertebrates. Size-classes are user defined and can also incorporate variation in taxonomic composition and energy density. While drift data may not always be available, we have found that the shape of standardized bioenergetic HSCs (as opposed to absolute NREI) are very robust to drift concentration (see user manual for detailed simulations); therefore, lacking drift data should not be a barrier to model application. Example drift data sets from Alaska and British Columbia are provided with the program.

Beyond generating basic bioenergetic HSCs, the software offers two additional capabilities. First, users can supply a file of depth and velocity point measurements (e.g., from transects) and the model will compute NREI, standardized habitat suitability, and all intermediate calculations (e.g., gross energy intake, swimming costs) at each point. This function allows users to directly generate estimates of NREI, swimming costs, or other metrics of habitat quality from field measurements or spatially explicit hydraulic model predictions. Second, users can specify ranges of input variables (e.g., fish size, temperature, drift concentration) and the software will return a separate bioenergetic HSC for each value across that range. This functionality allows straightforward sensitivity analyses of

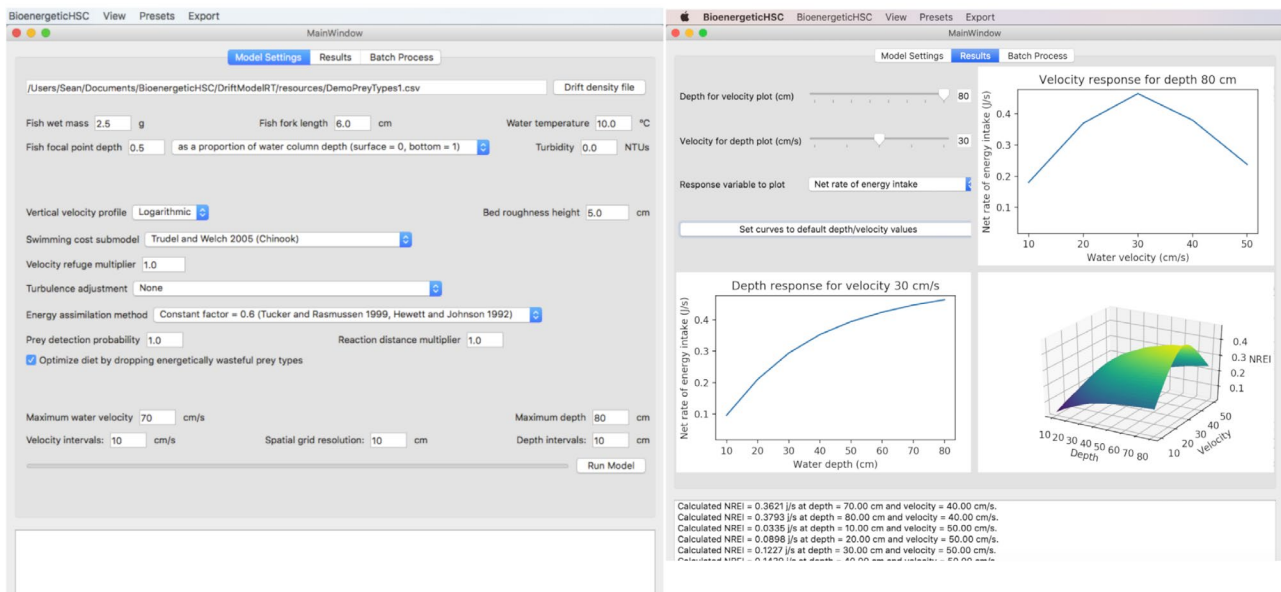


Figure 3. Screenshot of modelling software user interface. The only input data required to run the model are concentrations of discrete size classes of invertebrate drift, which are imported into the software as a .csv file. All other model specifications can be configured by the user in drop down menus, shown in the left panel. The right panel shows the model output, which can be viewed simultaneously. The displayed output shows the bivariate surface of habitat suitability across all depth and velocity combinations over ranges specified by the user as well as univariate curves where depth or velocity is held constant. All results can then be exported as .csv files.

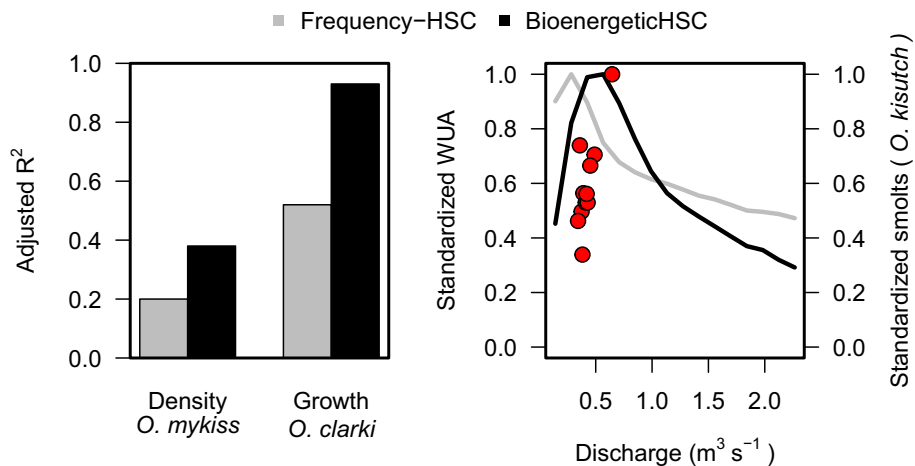


Figure 4. A summary of previous studies comparing frequency and bioenergetics-based habitat suitability curves (HSCs). The plot on the left shows the adjusted R² values from linear regression models relating habitat suitability (predicted with either frequency or bioenergetic HSCs) to relative steelhead fry density (fish/m²) and Coastal Cutthroat growth rates (% mass/day; see Naman et al. 2019 for details). The plot on the right shows standardized Coho smolt production estimates (red points) plotted as a function of summer low-flow discharge in Bingham Creek, WA; superimposed on this empirical smolt production vs. flow relationship are Weighted Usable Area estimates from PHABSIM calculated using either frequency (grey line) or bioenergetic-based (black line) HSCs (computed as combined habitat suitability × habitat area). The bioenergetic HSCs provide a superior fit to the smolt production (validation) data (see Rosenfeld et al. 2016 for additional details).

how HSCs are influenced by abiotic or biotic variables like turbidity or prey abundance and composition; we discuss the sensitivity analysis function in more detail in the following section.

ADVANTAGES OF BIOENERGETIC HABITAT SUITABILITY CRITERIA

Bioenergetics-based HSCs avoid several shortcomings of traditional frequency-based HSCs, including the potential biases associated with using observed habitat use as an indicator of habitat quality (Van Horne 1983). Because bioenergetic HSCs are based on fundamental linkages between physical

habitat and energy balance, they provide a consistent and objective metric of suitability that has a clear biological interpretation and should be applicable in principle to any system with drift-feeding fish. Bioenergetic HSCs should also be more transferable across locations relative to frequency-based HSCs generated from habitat use observations, which are sensitive to site-specific habitat availability, fish density, food abundance, and temperature. For example, bioenergetic HSCs could be rapidly applied to multiple streams that vary in productivity (assuming the relative differences in drift concentration are known) and could also be used to empirically rank their relative

Box 2 Application of bioenergetic HSCs in New Zealand.

Bioenergetics-based drift-foraging models have been used in New Zealand to inform ecological flow assessments for salmonids since 2015 and have been under research and development since the early 2000s (Hughes et al. 2003; Hayes et al. 2007, 2016). These complex applications linked one- or two-dimensional hydraulic models with drift transport and foraging models to provide spatially explicit predictions of net rate of energy intake (NREI) and reach-scale predictions of fish abundance as functions of flow and have complemented traditional methods for modeling flow requirements of salmonids. However, the high cost of these applications has incentivized uptake of the BioenergeticHSC software, which is more economically and computationally tractable at the expense of simplifying some key processes known to affect habitat selection and carrying capacity (e.g., local depletion of drift by foraging salmonids). Here we illustrate a recent application of BioenergeticHSC in New Zealand, where bioenergetic HSCs for drift-feeding Rainbow Trout are being used to complement ongoing habitat modeling using traditional frequency-based habitat suitability curves (HSCs; Hayes et al. 2019).

Instream flow modeling was conducted to assess the ecological effects of water withdrawal for a nationally important hydropower scheme on the Tekapo River (Figure 6), which was diverted at Lake Tekapo for the Waitaki Power Development in 1978 (Jowett and Biggs 2006). Previously, HSCs have not been developed for trout in the Tekapo River; consequently, frequency-based HSCs were borrowed from other systems, including the Tongariro River (North Island, New Zealand; I. Jowett, unpublished data) for yearling Rainbow Trout (10–20 cm) and the United States Rocky Mountain region (Wilding et al. 2014). Borrowing HSCs from other systems is routine in New Zealand, where few empirical HSCs for salmonids have been developed. However, because this practice can introduce considerable uncertainty, bioenergetic HSCs were developed to ground-truth suitability estimates and to reconcile potential differences among frequency-based HSCs. Bioenergetic HSCs were generated for 10- and 50-cm Rainbow Trout using a composite drift data set based on extensive sampling across New Zealand Rivers.

Bioenergetics modeling has provided several useful insights for interpreting frequency-based HSCs during the preliminary stages of the Tekapo River flow assessment. First, it confirmed that Rainbow Trout can forage profitably in deeper water than the Tongariro River depth suitability curve implies (Figure 7), broadly agreeing with Wilding et al. (2014) depth suitability curve. Second, the optimal velocity predicted by BioenergeticHSC for 50-cm Rainbow Trout matched the optima of the frequency-based velocity suitability curves, reinforcing the credibility of these predictions. However, the empirical frequency-based HSCs were more right skewed, suggesting that Rainbow Trout may be using complex hydraulics associated with large substrate (Hayes and Jowett 1994), allowing them to use higher average water column velocities than predicted with simple bioenergetics. Third, when the HSCs were integrated with a one-dimensional hydraulic habitat model using System for Environmental Flows Analysis software (Jowett et al. 2019), area weighted habitat suitability predictions based on bioenergetic criteria supported the inference that the present flow regime is close to optimal for adult Rainbow Trout (Figure 7).

In sum, bioenergetic HSCs reinforced the credibility of instream flow predictions for the Tepako River, while minimizing additional costs. Planned sensitivity analyses with BioenergeticHSC incorporating bed roughness, focal point depth, and drift concentration will further increase confidence around these predictions.

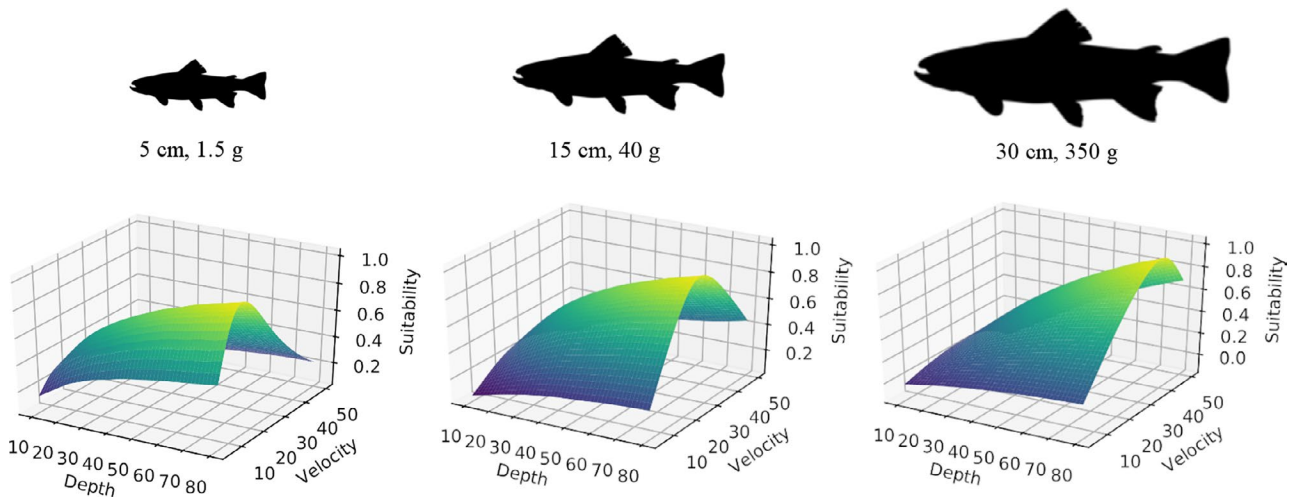


Figure 5. Examples of a possible sensitivity analysis of fish size using the software’s batch processing capabilities. Suitability surfaces for three sizes of fish are shown at 12 degrees Celsius. This type of sensitivity analysis could be used in combination with the Physical Habitat Simulation Model to explore how optimal flows shift as fish grow larger, and both their swimming costs and ability to use faster velocities change. Invertebrate drift data used for these simulations was from the Coquitlam River in southwest British Columbia, Canada (see Naman et al. 2019 for description).

productive capacities based on NREI; in contrast, traditional frequency-based approaches would require the development of separate HSCs based on observations in each stream, and maximum habitat quality in all streams would be fixed at unity.

The advantages of bioenergetic HSCs are also evident from direct comparisons of the two approaches against empirical data. For example, we previously demonstrated that bioenergetic HSCs made improved predictions of density of juvenile steelhead *Oncorhynchus mykiss* (anadromous

Rainbow Trout) and growth of Coastal Cutthroat Trout *O. clarkii clarkii* relative to frequency-based HSCs (Naman et al. 2019). Similarly, Rosenfeld et al. (2016) showed that flow requirements using bioenergetic HSCs matched Coho Salmon *O. kisutch* smolt production in a western Washington stream better than frequency-based HSCs, which systematically underestimated optimal flows (Figure 4). In addition to the well-documented ability of drift-foraging models to predict foraging locations (Hughes 1992), these case studies



Figure 6. Photograph of (a) the Tepako River, South Island, New Zealand, where instream flow modeling is being conducted to evaluate flow requirements for Rainbow Trout. Drift data inputs for bioenergetic HSCs came from a composite data set of drift measurements across New Zealand streams. Panel (b) shows an example of drift sampling. Note that this example shows vertically stacked drift nets, which are not necessarily required for the BioenergeticHSC software.

reinforce the utility of NREI as a robust indicator of habitat quality.

Bioenergetic HSCs also allow for sensitivity analyses that would not be possible using traditional HSC approaches. For example, by adjusting model parameters, one can examine the sensitivity of HSCs to environmental variables like turbidity that covary with flow or to biotic variables like prey abundance, prey composition, or fish size (Figure 5). When integrated into the broader PHABSIM framework, this could provide a powerful approach to explore how multiple interacting stressors influence fish habitat requirements. These sensitivity analyses

can also approximate more dynamic conditions inherent to river systems. For example, multiple HSCs generated across a gradient of body size could be used to explore how optimal flows change with ontogeny (Figure 5). Note that realistically simulating sensitivity of HSCs to temperature requires additional computations outside of the software to convert NREI from an instantaneous (J/s) to daily time scale (J/d). This is explained in detail in the user manual and will be addressed in future updates to the software.

Habitat suitability and NREI predictions from the software also have broader applications to stream habitat evaluation

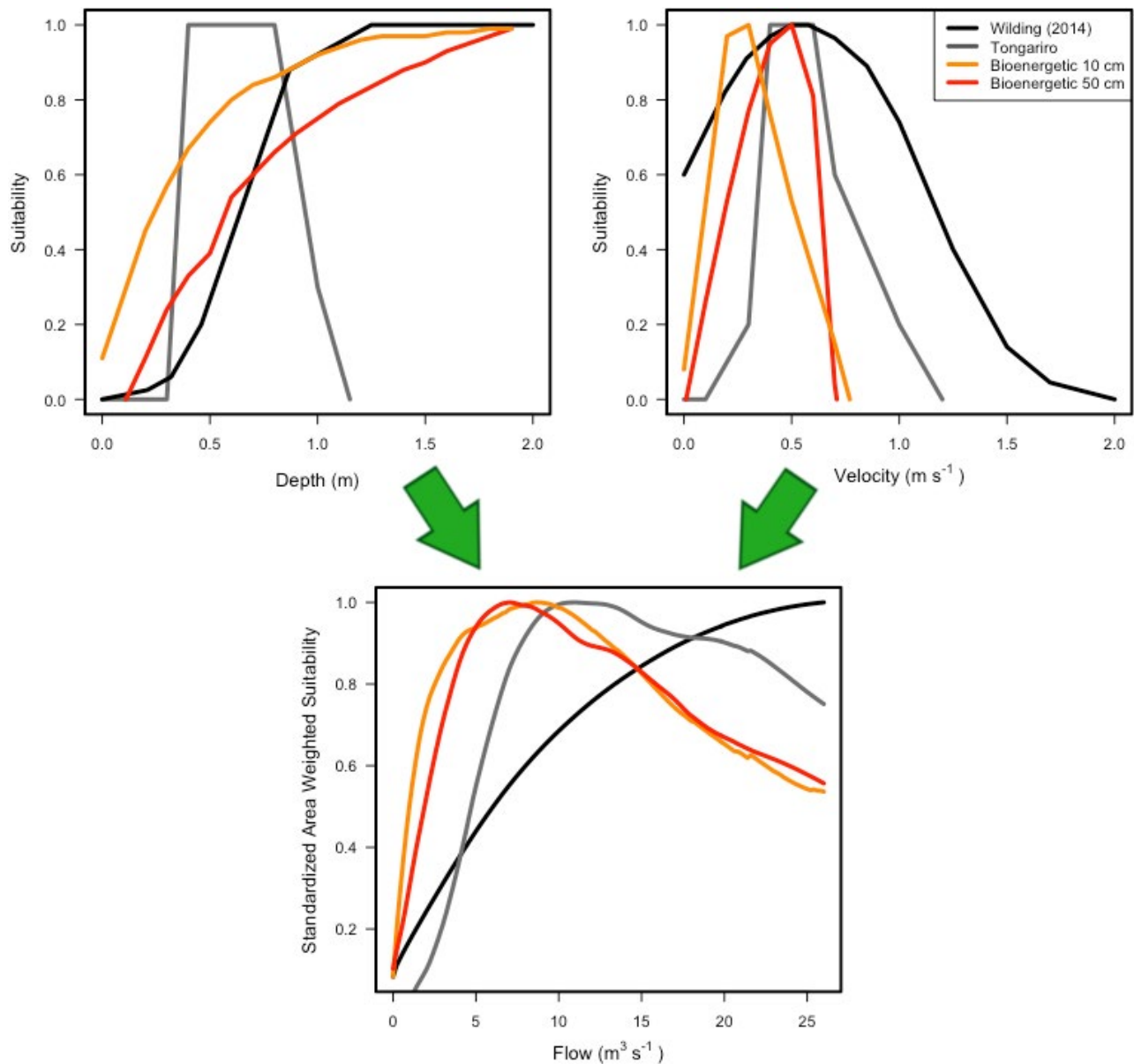


Figure 7. Comparison of depth and velocity HSCs (upper panels) and subsequent predictions of area weighted suitability across flow for Rainbow Trout in the Tepako River (lower panel). Frequency-based HSCs were borrowed from the Tongariro River, New Zealand, for 10–20-cm Rainbow Trout (I. Jowett, unpublished data) and from Colorado streams for Rainbow Trout and Brown Trout *Salmo trutta* greater than 17 cm (Wilding et al. 2014). Bioenergetic HSCs were developed for 15- and 50-cm Rainbow Trout and are displayed here in one dimension (depth is optimal in the velocity HSC plot and vice versa). Frequency- and bioenergetics-based HSCs were then linked to the one-dimensional hydraulic model in System for Environmental Flow Analysis to compute area weighted suitability (i.e., WUA)—the combined suitability index ($HSI_{depth} \times HSI_{velocity}$) in each hydraulic cell, weighted by cell area (see Jowett et al. 2019 for more details).

beyond instream flow modeling. For example, NREI computed by the program on user-supplied depth and velocity point measurements could be used as a rapid approximation of carrying capacity, based on the proportion of energetically profitable habitat (Wall et al. 2016). Similarly, it could also be used to test or predict the effectiveness of habitat restoration efforts aimed at increasing rearing capacity, (Hafs et al. 2014); (Keeley et al. 2016). The potential spatial scale of these applications is only limited by the quantity of hydraulic data and computing power.

Caveats

Our software is designed to facilitate the straightforward generation of bioenergetic habitat suitability criteria. However, appropriate application of drift-foraging models still critically requires understanding their assumptions and limitations. We strongly encourage users to consult the user manual for detailed guidance on when it is appropriate to apply bioenergetic HSCs and to read the original publications that describe drift-foraging bioenergetics models to understand how they work and their limitations (Hughes and Dill 1990; Hughes et al. 2003; reviewed in Piccolo et al. 2014).

We also emphasize that bioenergetic HSCs are still not completely free from some of the pitfalls and controversies associated with the broader PHABSIM framework (Railsback 2017). For example, bioenergetic HSCs are not fully spatially explicit (discussed in Naman 2019) and do not currently account for biotic factors, such as predation risk and competition, which can strongly affect habitat quality. They also do not make dynamic population-level predictions, which are arguably the gold standard for instream flow modeling (Anderson et al. 2006), although direct NREI estimates from the software could provide computationally efficient inputs to more complex mechanistic models linking flows to growth potential and population dynamics (e.g., McHugh et al. 2017).

CONCLUSION

Ultimately, the utility of any instream flow modeling tool will be determined by logistical constraints, available resources, and the quality of the hydraulic and biological data available for any given system. For the many cases where application of more complex mechanistic models is not feasible, bioenergetic HSCs should provide a useful tool to improve the rigour and credibility of instream flow assessments by providing a mechanistic substitute for frequency-based HSCs or as a complementary approach (Box 2). By providing a transparent and well-documented platform for generating bioenergetic HSCs, our software should lower the technical barriers to their judicious application to instream flow modeling.

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