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ORIGINAL ARTICLE

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Comparing correlative and bioenergetics-based habitat suitability models for drift-feeding fishes

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Abstract

1. Quantitative habitat suitability models (HSMs) are frequently used to inform the conservation and management of lotic organisms, often in the context of instream flow management. Correlative statistical models relating hydraulic variables to habitat preferences (habitat suitability curves based on use:availability ratios) are the most common form of HSM, but face significant criticism on the grounds that habitat preference may not reflect the fitness consequences of habitat use. Consequently, there has been a drive to develop mechanistic approaches that link habitat to direct correlates of fitness.
2. Bioenergetic foraging models relating hydraulic conditions to energy balance are particularly well-developed for drift-feeding fishes (e.g. salmonids) and show promise as a more mechanistic approach to modelling suitability. However, these models are rarely validated empirically or quantitatively compared with correlative HSMs. We addressed these gaps by comparing the ability of a bioenergetics-based HSM and two correlative HSMs (a traditional suitability index and a resource selection function) to predict density and growth of stream salmonids (juvenile steelhead, *Oncorhynchus mykiss*, and coastal cutthroat trout, *Oncorhynchus clarki*).
3. Suitability estimates differed between the approaches, with both correlative models predicting higher suitability relative to the bioenergetic model at shallow depths and low to intermediate velocities, but lower suitability as depth increased. The bioenergetic model explained over 90% of variation in trout growth, compared to *c*. 50% for the correlative model. The bioenergetic model was also better at predicting fish density; however, the improvement was less striking and a high proportion of variation remained unexplained by either method.
4. Differences in suitability estimates between approaches probably reflect biotic interactions (e.g. territorial displacement or predation risk) that decouple realised habitat use from energetics-based estimates of habitat quality. Results highlight fundamental differences between correlative HSMs, based on observed habitat use, and mechanistic HSMs, based on the physiology and behaviour of the focal taxa. They also suggest that mechanistic bioenergetics-based models provide more rigorous estimates of habitat suitability for drift-feeding stream fishes. The bioenergetics approach is readily accessible to instream flow practitioners because model predictions are expressed in terms of traditional habitat suitability curves.

KEYWORDS
foraging, instream flows, mechanistic model, PHABSIM, Salmon

1 | INTRODUCTION

Quantitative models for evaluating habitat suitability are critical for effective natural resource management and conservation. Habitat suitability models (HSMs) take a variety of forms but can be generally grouped into two distinct classes: correlative habitat selection or preference models and mechanistic niche models. Correlative models determine suitability by statistically relating habitat features to the occurrence or density of a target species (Boyce & McDonald, 1999; Manly, McDonald, Thomas, McDonald, & Erickson, 2007). In contrast, mechanistic models determine suitability by linking habitat features to more direct fitness correlates, such as, energy balance, growth, or survival, premised on fundamental knowledge of a target species' physiology or behaviour (Kearney & Porter, 2009). Because mechanistic HSMs more explicitly link habitat to fitness, they arguably provide a more robust and transferable approach for predicting biological responses to habitat change (Cuddington et al., 2013; Kearney, Simpson, Raubenheimer, & Helmuth, 2010). However, model practitioners with limited time and resources are often constrained by computational complexity and the scope and detail of information required to make predictions. Consequently, despite the rapid advancement of mechanistic HSMs for an array of taxa, simple correlative approaches are often used in lieu of more mechanistic ones (Meineri, Deville, Grémillet, Gauthier-Clerc, & Béchet, 2015). This disjunction between model development and application is especially evident in stream ecosystems, where correlative HSMs are routinely applied to navigate trade-offs between fish habitat requirements and water allocation for human use (Anderson et al., 2006).

Habitat assessments for stream fishes often rely on standardised suitability indices for physical habitat variables such as depth and velocity, which are then integrated with hydraulic models to make predictions of how fish habitat availability responds to changes in stream flow or channel structure (Ahmadi-Nedushan et al., 2006; Lamouroux, Hauer, Stewardson, & LeRoy Poff, 2017). This approach is particularly integral to the physical habitat simulation model (PHABSIM; Bovee et al., 1998), a widely used framework for predicting biological responses to changing discharge to inform instream flow management decisions. Suitability indices for these applications can be developed in different ways (Dunbar, Alfredsen, & Harby, 2012). Most often, they are defined by habitat suitability curves (HSCs), which are simple correlative models based on observed frequency of microhabitat use. Habitat suitability curves are generated by dividing the frequency of use for different microhabitat conditions (e.g. depth) by habitat availability to produce a univariate selection index that is standardised to a maximum of one (e.g. Beecher, Thorn, & Carleton, 1993). A combined suitability metric is then computed as the product of standardised suitability indices for each habitat variable considered.

While HSCs based on use:availability ratios are computationally and conceptually convenient, they have seen little change since their initial development, and have been strongly criticised as being out of step with modern habitat modelling techniques (Railsback, 2016). Many have advocated for more statistically rigorous approaches that consider habitat selection as a multivariate process and incorporate covariance and interactions among habitat variables (e.g. Beakes et al., 2014; Guay et al., 2000). Numerous methods for this are available, including probabilistic resource selection functions (RSFs) developed in the terrestrial wildlife literature (Boyce & McDonald, 1999); however, they are all ultimately correlative. A deeper issue that no correlative HSM can resolve is that habitat preference may be a poor indicator of the fitness consequences of habitat use (Garshelis, 2000), especially for territorial animals like many stream fishes where subordinate individuals are often displaced into lower quality habitats at high densities (Railsback, Stauffer, & Harvey, 2003; Van Horne, 1983). Mechanistic models that link habitat conditions to individual-level fitness can address this issue (e.g. Railsback, Harvey, Jackson, & Lamberson, 2009; Van Winkle et al., 1998), but the complexity of these approaches has limited their use by practitioners (Reiser & Hilgert, 2018).

For stream fishes that feed on drifting invertebrates (e.g. salmonids), bioenergetics-based foraging models provide a useful intermediate step between correlative HSMs and more complex mechanistic approaches (e.g. Railsback et al., 2009). Drift-foraging bioenergetics models describe the energetic consequences of foraging as a function of the hydraulic environment, temperature, and prey abundance, ultimately estimating habitat quality in terms of net energy intake (NEI), i.e. the balance between energetic costs and benefits in different habitat conditions (Fausch, 1984; Hughes & Dill, 1990; Piccolo, Frank, & Hayes, 2014). While NEI is not an explicit measure of fitness *per se* and there are issues directly translating model estimates to predict growth, NEI does effectively rank relative habitat quality (Rosenfeld, Bouwes, Wall, & Naman, 2014). Thus, it provides a metric of suitability that causally links habitat conditions to potential energy gain, which is an improvement over correlative suitability metrics that often lack a clear ecological interpretation (Addley, 1993; Hayes, Goodwin, Shearer, Hay, & Kelly, 2016). Consequently, bioenergetics-based HSMs have been gaining traction in applied contexts (e.g. Bouwes, Bennett, & Wheaton, 2016) and numerous iterations of the approach have been developed (Piccolo et al., 2014; Rosenfeld et al., 2014). These include converting bioenergetic predictions into standardised suitability indices for water velocity and water depth (hereafter: *velocity* and *depth*) as a simple mechanistic alternative to correlative indices within the PHABSIM modelling framework (Braaten, Dey, & Annear, 1997; Rosenfeld, Beecher, & Ptolemy, 2016).

Regardless of whether habitat suitability indices are defined by simple use, availability ratios, occupancy probability, or energy balance, there is an implicit assumption that indices accurately represent fish abundance and/or performance. This assumption is rarely confronted, especially for bioenergetic HSMs where model development has outpaced empirical validation (but see Urabe, Nakajima, Torao, & Aoyama, 2010; Wall, Bouwes, Wheaton, Saunders, & Bennett, 2016). In addition, correlative and bioenergetic HSMs are rarely directly compared, making it difficult to quantify their respective benefits and limitations. We addressed these gaps by comparing correlative and bioenergetic HSMs both in terms of their predicted habitat suitability values and their ability to predict observed density and growth of juvenile salmonids across a gradient of habitat conditions. We specifically contrasted three models: (1) a mechanistic bioenergetic drift-foraging model; (2) a simple correlative model based on the product of univariate HSCs for depth and velocity (hereafter: *HSC-based model*), as typically used in instream flow assessments; and (3) a more statistically rigorous (but still correlative) RSF based on a generalised linear model that incorporates multiple habitat variables simultaneously.

We predicted that biotic interactions might cause suitability estimates from both correlative models to diverge from the density-independent bioenergetic predictions. In particular, we expected that correlative models would over-estimate habitat suitability relative to the bioenergetic model due to territorial displacement of subdominant fish into energetically unfavourable habitat, e.g. very slow velocities and shallow depths (Nielsen, 1992). Territoriality is frequently observed in stream salmonids (Nakano, 1995) and probably exerts a strong influence on correlative HSMs (Beecher, Caldwell, DeMond, Seiler, & Boessow, 2010; Orth, 1987; Rosenfeld, Leiter, Lindner, & Rothman, 2005). With respect to HSM performance predicting density and growth, we predicted that: (1) the bioenergetics model would outperform both correlative models given that it incorporates the fundamental mechanisms linking habitat to energy intake and swimming costs; (2) the RSF would outperform the HSC-based model due to its enhanced statistical rigor; and (3) bioenergetic suitability estimates would predict growth better than density, since the mechanistic relationship between modelled net energy intake and growth is more direct, whereas additional influences (e.g. predation risk, competition) can complicate the link between net energy intake estimates and density.

2 | METHODS

Two independent validation data sets were used to address our objectives. First, we generated correlative HSMs and parameterised the bioenergetic model with field observations of juvenile steelhead (*Oncorhynchus mykiss*) microhabitat use and abundance, invertebrate drift, and hydraulic attributes from two streams. We then compared suitability estimates among the three HSMs as well as their ability to predict steelhead density at the channel unit scale. Second, we used data from an earlier field experiment (Rosenfeld & Boss, 2001) to compare how well the contrasting HSMs (specifically the bioenergetic versus HSC model) could predict density-independent growth of coastal cutthroat trout (*Oncorhynchus clarki*) in experimental enclosures. We elaborate further on these procedures below but first describe our bioenergetics-based HSM.

2.1 | Bioenergetics-based HSM

Our bioenergetics-based HSM is premised on the drift-foraging bioenergetics model from Rosenfeld and Taylor (2009) and Hughes, Hayes, Shearer, and Young (2003), which built on the foundational work by Fausch (1984) and Hughes and Dill (1990). Drift-foraging bioenergetics models essentially describe how velocity and depth influence the geometry of prey detection and capture for fish in flowing water, while also accounting for the energetic costs of swimming, maneuvering to capture prey, and metabolism. The ultimate currency of the model is instantaneous NEI (J/s), which is computed as gross energy intake less the combined energy costs. Gross energy intake is determined by invertebrate drift concentration (number/m^3), size-dependent reaction distances of a fish to discrete size classes of invertebrates, and the total flux of drift through a fish's reaction volume. Energy costs of swimming and maneuvering are primarily functions body size, temperature, and water velocity (Table 1).

Further details of the modelling approach are well described elsewhere (see Rosenfeld & Taylor, 2009; Rosenfeld et al., 2014); however, our model differs from earlier efforts in several ways. First, NEI calculations in most drift-foraging models are made on a series of grid cells within a teardrop-shaped reaction volume that extends from a fish's focal point out to the maximum distance it can detect and capture prey. To match the circular volume boundary, cells at the edges are wedge-shaped (Hughes et al., 2003). In contrast, our model treats the foraging volume as a symmetric grid of 5 cm^2 cells on the plane of the focal point that extend upstream to the reaction distance; cells are included in the reaction volume if their centres fall within the maximum capture distance. This approach was motivated by our goal of building bioenergetic HSCs from depth and velocity alone, as opposed to mapping NEI across a channel with known geometry. It also still approximates a hemispherical foraging volume while considerably simplifying its calculation. However, by using a symmetric grid the model cannot account for irregularly shaped foraging volumes or lateral velocity gradients within a fish's reactive field (Guensch, Hardy, & Addley, 2001; Hughes et al., 2003). Second, our model includes a novel diet optimisation algorithm to account for fish ignoring low-quality prey items that would not increase their overall NEI. Following the logic of optimal foraging theory (Charnov, 1976), the model performs the full NEI calculations with and without each prey category, then removes a prey category if a fish's NEI would be higher without it (i.e. if costs of prey acquisition exceed benefits). This process is repeated until a full cycle over all prey categories is completed without any additional removals. This feature

TABLE 1 Components of the drift-foraging bioenergetics model

Parameter	Definition	Method	Reference/Source
T	Temperature (°C)	Field data	
V	Velocity (cm/s)	Field data	
i	Prey length class within l 1-mm bins	Field data	
j	Subscript denoting one 5-cm^2 cell	This model	
J	Total number of cells in foraging volume	This model	
FL	Fork length (cm)	Field data	
$Conc_i$	Concentration of prey class i	Field data	
EC_i	Energy content of prey class i	Published conversions	Benke et al. (1999); Cummins and Wuycheck (1971)
$PL_{\min}$	Minimum prey length in diet (mm)	$PL_{\min} = 0.115FL$	Wańkowski (1979)
$PL_{\max}$	Maximum prey length in diet (mm)	$PL_{\max} = 4.415FL$	Wańkowski (1979)
RD_i	Reaction distance (cm) to prey class i	$RD_i = 0.12PL(1 - e^{-0.2FL})$	Hughes and Dill (1990)
$V_{\max}$	Maximum sustainable swimming speed (cm/s)	$V_{\max} = 36.23FL^{0.19}$	Wańkowski (1979)
V_{opt}	Optimal swimming speed (cm/s)	$V_{\mathrm{opt}} = 17.6\ \mathrm{mass}^{0.05}$	Hughes and Dill (1990)
MCD_i	Maximum prey capture distance (cm)	$MCD = (RD_i^2 - (V * RD_i / Vmax^2)^{0.5})$	Wańkowski (1979)
CS	Prey capture success proportion	$CS = e^u/(1 + e^u)$	Rosenfeld and Taylor (2009)
		$u = 1.28 - 0.0588V + FL$	Rosenfeld and Taylor (2009)
		$-0.0918(Depth/RD)$	Rosenfeld and Taylor (2009)
		$-0.210V(Depth/RD)$	
SC	Focal swimming cost (J/s)	$SC = a(mass)^{b1}e^{b2T}e^{b3(0.01V)}(4.2/86{,}400)$	Hayes et al. (2016)
PD	Pursuit distance (cm)	$PD_i = (2/3)RD_i$	Hayes et al. (2016)
PT	Pursuit time (s)	$PT = PD/V$	Hayes et al. (2016)
RT	Return time to focal point (s)	$RT = PD/V_{\mathrm{opt}}$	Rosenfeld and Taylor (2009); Hayes et al. (2016)
PS	Scaler for pursuit in unsteady flow	$PS = (3V^2)^{0.5}$	Hayes et al. (2016)
RS	Scaler for return in unsteady flow	$RS = (3V_{opt}^2)^{0.5}$	Hayes et al. (2016)
TS	Scaler for energy costs of turning	$TS = 0.978\mathrm{e}^{0.002\mathrm{V}}$	Hayes et al. (2016)
MC	Energy costs of maneuvering (J)	$MC = (PT)(SC)(PS) + (RT)(RS)(TS)$	Hayes et al. (2016)
ER	Total prey encounter rate (n/s)	$ER = 2(\sum_i^j I100V_jCONC_i)$	Hughes et al. (2003)
EI	Total energy intake (J)	$EI = \sum_i^j ICS_jER_jEC_i$	Hughes et al. (2003)
EIA	Total energy intake assimilated (J)	$EA = EI(0.7(EI/1 + PT))$	Hughes et al. (2003)
TT	Total searching and handling time (s)	$TT = 1 + PT$	Hughes et al. (2003)
GEI	Gross energy intake rate (J/s)	$GEI = EI/TT$	Hughes and Dill (1990)
EC	Total energy costs (J/s)	$EC = SC + MC$	Hughes and Dill (1990)
NEI	Net energy intake rate (J/s)	$NEI = GEI - EC$	Hughes and Dill (1990)

of the model is particularly influential in preventing unrealistically negative NEI values under conditions where drift-feeding is not energetically profitable (Rosenfeld et al., 2014).

We used predicted NEI from the bioenergetics model to generate standardised habitat suitability criteria following Rosenfeld et al. (2016). Using invertebrate drift concentrations, fish size, and water temperature as inputs, the model computes NEI across all combinations of depth and velocity over a user-specified range, creating a bivariate NEI surface (Figure 1). Net energy intake rate values are then standardised to a maximum of 1 by dividing each value by the overall maximum. To allow comparison with correlative HSMs that make predictions on a 0–1 scale, negative bioenergetic suitability values are set at 0. This effectively assumes all conditions where a fish would experience an energy deficit are equally unsuitable (Rosenfeld et al., 2016). The model was built in Python (version 3.3) and is designed as a graphical user interface-based tool to generate bioenergetic indices of habitat suitability (preliminary version available at https://github.com/JasonNeuswanger/BioenergeticHSC).

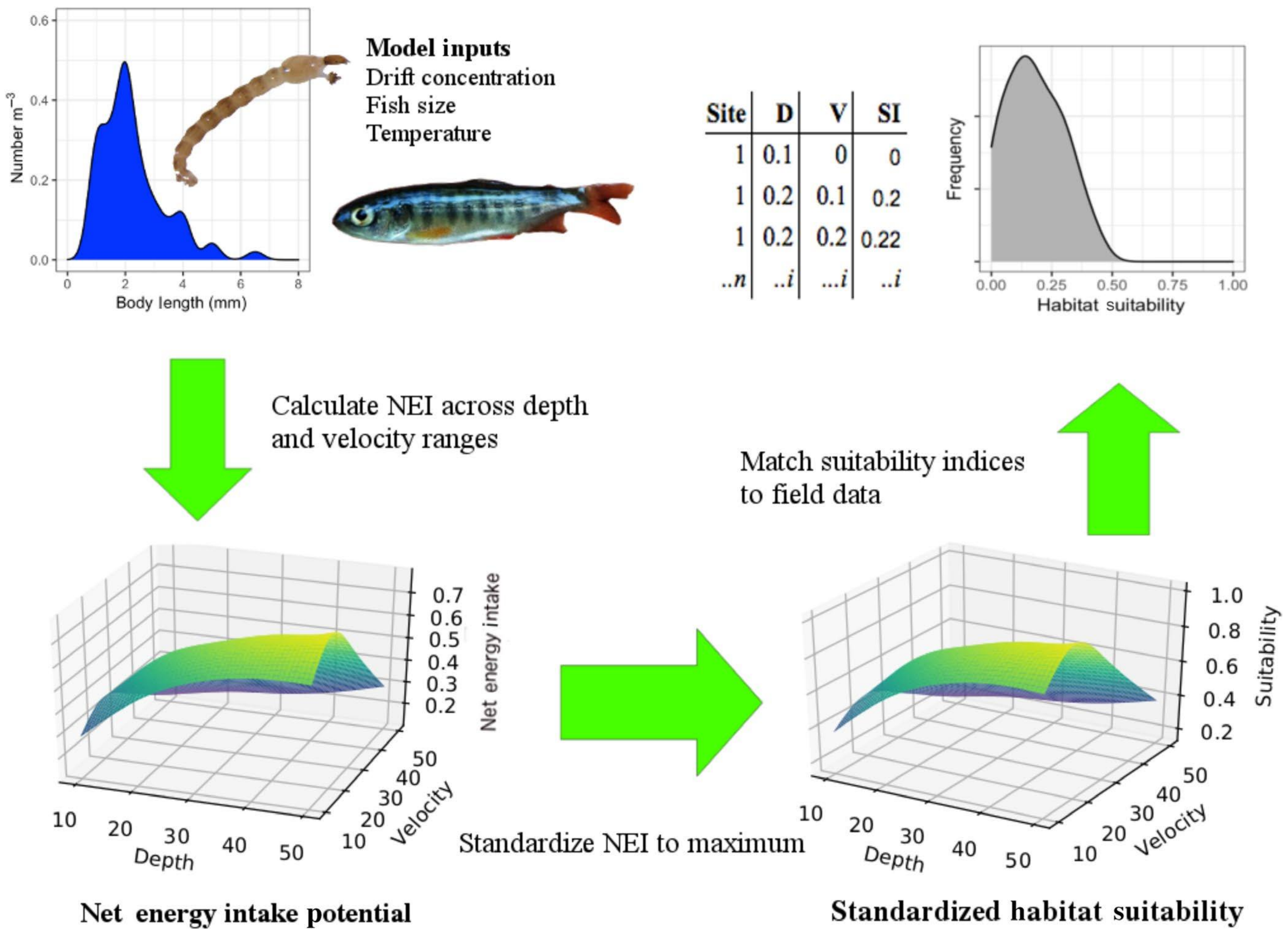

FIGURE 1 Conceptual diagram of the bioenergetic habitat suitability modelling approach. The model is initially parameterised with concentrations of invertebrate drift (in 1-mm length bins), fish length and mass, and temperature. The model then computes net energy intake (NEI) across all combinations of depth and velocity within a specified range, creating a three-dimensional NEI surface. This surface is standardised to a maximum of 1 by dividing all NEI values by the global maximum. These standardised suitability values are then matched to field measurements of depth and velocity and aggregated to characterise the distribution of habitat suitability over a larger scale; for example, the figure in the top right corner is a riffle from Silver Hope Creek, BC, Canada

TABLE 2 Mean attributes of each sampled reach. Except for the total area sampled, values are the mean among channel units. Dominant substrate types are based on visual classification during depth and velocity transects. Discharge and temperature data are averaged for the duration of our sampling. Densities and fork lengths are only for steelhead fry

Stream	Reach	Total area (m^2)	Unit area (m^2)	Substrate	Q (m^3/s)	Temp. (°C)	n/m^2	g/m^2	FL (mm)
Coquitlam	1	1,297.59	43.25	Cobble–Boulder	2.40	17.50	1.10	1.21	44.36
Silver Hope	1	882.69	51.92	Gravel–Cobble	0.38	10.54	0.87	1.78	54.98
Silver Hope	2	465.39	33.24	Cobble–Boulder	0.30	10.30	0.41	1.00	60.03

2.2 | Habitat suitability curves

We used standard instream flow methodology to develop the correlative HSC-based model by directly measuring juvenile steelhead microhabitat preferences, i.e. depth and velocities used relative to depths and velocities available in the environment. Data were collected in August and September from the Coquitlam River (49.3370′ N, −122.770′ W) and Silver Hope Creek (49.2600′ N, −121.3970′ W), two tributaries to the lower Fraser River in Southwest, British Columbia, Canada (site attributes presented in Table 2). Both systems contain populations of resident and anadromous *O. mykiss* and several other fish species; coho (*Oncorhynchus kisutch*), mountain whitefish (*Propesium williamasi*), speckled dace (*Rhinichthys osculus*), and sculpins (*Cottus* spp.) occur in the Coquitlam, while low densities of bull char (*Salvelinus confluentus*) occur in Silver Hope. Several of these species are also drift-feeders but were not sufficiently abundant to reliably estimate density. In the absence of information on length–age relationships, we distinguished steelhead fry (0+) from parr (1+) using a threshold of 75 mm that corresponded to distinct breakpoints in length-frequency histograms for both streams. All results were insensitive to this cut-off within ± 20 mm.

We conducted steelhead microhabitat observations in a discrete *c*. 200-m long reach in the Coquitlam, and two separate *c*. 100-m long reaches of Silver Hope Creek. To measure steelhead microhabitat use, a snorkelling observer moving upstream would carefully mark the location of undisturbed fish, where a second observer would then measure the depth and mean water column velocity (60% of the water depth; 20% and 80% if depth exceeded 1 m). We estimated habitat use for 256 steelhead fry, 174 in the Coquitlam and 82 in Silver Hope (two reaches combined). We quantified habitat availability by delineating each reach into constituent channel units (e.g. riffle, pool, run, and glide; Frissell, Liss, Warren, & Hurley, 1986), and measuring transects of depth and average water column velocity using a top-set wading rod and Marsh McBirney flow meter (Hach Corporation). Measurement points were spaced 20 cm apart on each transect and longitudinal transect spacing varied between 20 and 50 cm depending on the channel unit area. This transect spacing approximated the reaction distance (18–24 cm) of steelhead in our study calculated from the drift-foraging model and was also similar to previous methodology used to construct correlative habitat suitability criteria (Beecher et al., 2010).

Reach-scale habitat availability was computed by summing all transect points, which were weighted by the proportion of stream area they represented (Beecher et al., 1993). We determined scaled habitat preferences for depth and velocity in each reach by dividing proportional use by availability, then standardising to a 0–1 scale by dividing each preference value by the maximum. Because of low sample sizes, the two Silver Hope reaches were combined for this analysis. Smoothed suitability curves for velocity and depth in each stream were then derived by fitting probability density functions with L-moments distribution statistics using the R package *lmomco* (Som, Goodman, Perry, & Hardy, 2015). In all cases, the Weibull distribution was selected over several other candidate probability density functions (Gamma, exponential, and Rayleigh) based on its higher maximum likelihood. Habitat suitability curves generated with this method were qualitatively similar to other commonly used approaches including kernel density smoothers (Hayes & Jowett, 1994) and univariate logistic regressions (Ayllón, Almodóvar, Nicola, & Elvira, 2012).

2.3 | Multivariate RSFs

As a more statistically rigorous correlative HSM, we developed probabilistic RSFs, a form of HSM that describes the relative probability that habitat features are used in relation to their availability (Boyce & McDonald, 1999). We constructed RSFs for steelhead in each stream by creating matrices of relative preference for every unique combination of depth and velocity (Coquitlam: n = 1,294; Silver Hope: n = 1,084), then fitting a generalised linear model with a quasibinomial error distribution and log link function using the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015). This approach for RSFs is analogous to logistic regression using presence–absence data (Manly et al., 2007). We fit both linear and second-order polynomial terms as well as interactions and tested significance with nested likelihood ratio tests based on the χ^2 distribution (Zuur, Leno, Walker, Saveliev, & Smith, 2009). We used the RSFs to predict habitat use probabilities across all combinations of depth and velocity observed in the field, then standardised probabilities to a 0–1 scale to be consistent with other HSMs (Ayllón et al., 2012). Substrate size and presence of cover were measured in the field but were not significant predictors in the RSFs and did not influence HSC-based suitability predictions, and thus were not included in subsequent analysis.

2.4 | Comparison of model performance

To compare the ability of the three HSMs (bioenergetics, correlative HSCs, and the multivariate RSF) to predict steelhead density, we identified discrete geomorphic channel units within the designated reaches based on homogeneity of depth and velocity. We then estimated the density of steelhead fry in each channel unit (n = 45; 22 in the Coquitlam, 23 in Silver Hope) by either snorkelling or electrofishing depletion. Snorkelling was conducted in channel units with depths exceeding 20 cm. Starting from downstream, one observer would move upstream in a zig-zag pattern while enumerating fish and estimating their body length to the nearest 10 mm using markings on their glove as a reference. Means and standard errors of abundance estimates were computed based on 3–5 replicate snorkels for each unit. To increase the accuracy of snorkel estimates, we approximated stream-specific detection efficiencies with mark–recapture (Korman, Decker, Mossop, & Hagen, 2010). Steelhead collected outside the study reach (n = 5–10) were marked with a small strip of elastomer (Northwest Marine Technology) injected under the dorsal fin, then released into channel units (n = 2 per stream) prior to snorkelling. The elastomer tag was designed to be visible once a fish was seen without increasing the likelihood a fish would be detected, as would a larger tag. We then snorkelled through each habitat unit 6–8 hr after releasing fish as well as in directly adjacent units to ensure fish movement did not bias estimates. Abundance was then corrected for efficiency (Coquitlam = 0.87; Silver Hope = 0.56).

In shallow units, we estimated steelhead abundance using multi-pass electrofishing depletion. Channel units were completely enclosed with 5-mm mesh nets to prevent biases associated with fish movement (Wathen, Weber, Bennett, Bouwes, & Jordan, 2017), then sampled until either zero fish were caught or the number of fish caught decreased for three successive passes. Low conductivity precluded electrofishing in two channel units in the Coquitlam, so depletion procedures were conducted using pole seines. Captured fish were anaesthetised with tricaine methanesulfonate, measured to the nearest 1 mm and weighed to the nearest 0.1 g. Abundance was estimated for each channel unit using the maximum likelihood method for closed populations following Carle and Strub (1978) implemented in the R package *FSA* (Ogle, 2018). Abundance was estimated by both snorkelling and electrofishing in a subset (n = 7) of channel units to determine whether methods were comparable, which indicated a close correspondence in population estimates with no strong directional bias ($r = 0.81$).

We characterised the hydraulic environment within each channel unit by measuring transects of depth and velocity as described above, which resulted in 80–200-cm depth and mean water column velocity observations per unit. Temperature was recorded every 15 min in each reach using Onset HOBO temperature loggers (Onset Computing Corporation). To parameterise the bioenergetics model, invertebrate drift was measured at three or four locations within each reach ($n = 36$ total samples). Sampling at each location involved setting two adjacent drift nets (306 cm^2 opening, 250-μm mesh) for two replicate 30–45 min periods between 10h00 and 14h00. Filtration efficiency, estimated from the ratio of velocity at the beginning relative to the end of the sampling period, was always above 95%. Drift samples were preserved in 75% ethanol, then invertebrates were separated from debris under a dissecting microscope in the laboratory at 10× magnification, identified to order, and measured to the nearest 0.1 mm using an ocular micrometer. We computed drift concentrations by dividing the number of invertebrates in each 1-mm body length class by the volume of water filtered, then estimated dry mass and energy content using order-level conversion equations (Benke, Huryn, Smock, & Wallace, 1999; Cummins & Wuycheck, 1971).

Habitat suitability was estimated for all transect points within each channel unit. For the bioenergetics approach, we estimated habitat suitability at each point by parameterising the model with reach-averaged invertebrate drift concentration, fish size, and daytime temperatures in each stream. We set the focal point of fish at 80% of the water depth (i.e. 20% off of the stream bottom) to match snorkel observations (S. Naman, unpublished data) and assumed a logarithmic vertical velocity profile (Hayes, Hughes, & Kelly, 2007). Bioenergetic habitat suitability was then modelled across all combinations of depth (0–2 m) and velocity (0–2 m/s) at 0.01 (m or m/s) intervals to correspond to the depth and velocity ranges measured in the field, then suitability values were matched to each transect point. For the HSC model based on microhabitat use frequency, we computed a composite suitability index at each point using the product equation: $HSI_{\text{Composite}} = HSI_{\text{Depth}} \cdot HSI_{\text{Velocity}}$, where HSI_i is the depth or velocity suitability index from the HSC generated from our microhabitat observations. Finally, for the RSF, we matched standardised suitability predictions for the depth and velocity combination at each transect point.

To compare channel unit-scale habitat suitability to observed fish density, we aggregated suitability values in two ways: first, as the mean suitability value across all points in a channel unit, and second, as the proportion of points in each channel unit with suitability values above 0, which approximates the area of usable habitat in a channel unit. For instance, a larger proportion of above-zero bioenergetics-based suitability indicates a larger proportion of area where fish can achieve a positive energy balance (Wall et al., 2016).

To assess the performance of contrasting HSMs in predicting salmonid growth, we used data from Rosenfeld and Boss (2001), who measured the growth of cutthroat trout fry (40–60 mm FL) and parr (120–160 mm FL) that were enclosed at low densities in pool or riffle habitats in a natural stream. Individual growth rates were measured over 27 days and observations of focal foraging depths and velocities were made from the stream bank. Invertebrate drift was also collected using similar methods to those we described (see Rosenfeld & Boss, 2001 for complete description of experiment). With this information, we parameterised the bioenergetics model and predicted habitat suitability at each focal depth and velocity. Correlative HSMs were not available for the specific study stream so we used published suitability curves for coastal cutthroat trout in British Columbia; curves for parr came from Heggenes, Northtote, and Peter (1991) and curves for fry came from Burt and Horchik (1998). Habitat suitability curve-based suitability indices for each focal point were computed as the product of suitability curves for depth and velocity as described above. Bioenergetic and correlative suitability estimates were then used as independent predictors of the mean growth (% mass/day) of fish in each enclosure. Bioenergetic estimates were normalised relative to fish mass (i.e. NEI/g) in order to compare suitability of fry and parr on the same scale. Because only univariate suitability curves were available, we were unable to construct RSFs; consequently, only bioenergetic and HSC-based HSMs were compared in this analysis.

2.5 | Statistical analysis

All statistical analyses were conducted in R version 3.3.2 (R Core Development Team). To determine the extent that suitability estimates differed among HSMs, we examined pairwise correlations between suitability estimates from the three contrasting HSMs for all transect points of depth and velocity from our field surveys. Differences were further examined by comparing three-dimensional surfaces of habitat suitability estimated across all possible combinations of depth and velocity within their observed ranges. We then used two-sample Cramer tests to make pairwise comparisons of these suitability surfaces within each stream. The Cramer test is a non-parametric analogue of the Kolmogrov–Smirnov cumulative distribution test, which we extended for multivariate distributions following Baringhaus and Franz (2004), implemented in R using the *cramer* package (Franz, 2004). We derived critical test statistic values using a Monte-Carlo procedure based on 10,000 bootstrap replicates and used a Bonferroni correction to adjust p-values for false discovery rates.

We evaluated the ability of the three contrasting HSMs to predict steelhead density at the channel unit scale using ordinary least squares regression. Density was standardised relative to the mean of each reach and was natural log transformed to meet normality assumptions, which were verified with residual plots. We assessed the significance of predictors based on whether 95% confidence intervals around the slopes overlapped zero. We used a similar ordinary least-squares approach to test whether HSM suitability estimates could predict cutthroat trout growth (% mass/day). We assessed the overall performance of contrasting HSMs based on which explained the highest proportion of variation in density or growth, i.e. based on the highest R^2.

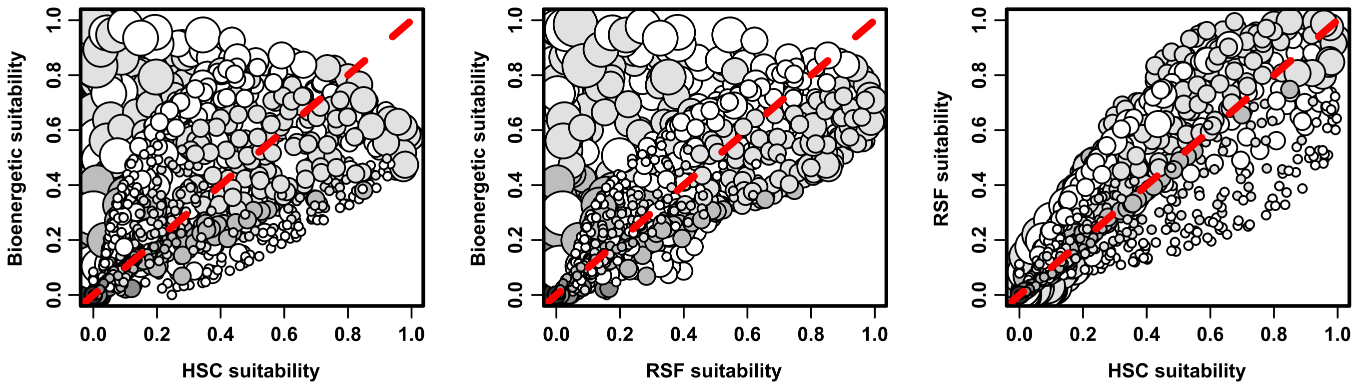

FIGURE 2 Pairwise correlations among correlative and bioenergetic habitat suitability models. The red dashed line represents a 1:1 relationship. The sizes of points represent the relative depth (m) and the shading of points represents relative velocity, i.e. larger and darker points represent deeper and higher velocity sites. HSC, habitat suitability curve; RSF, resource selection function

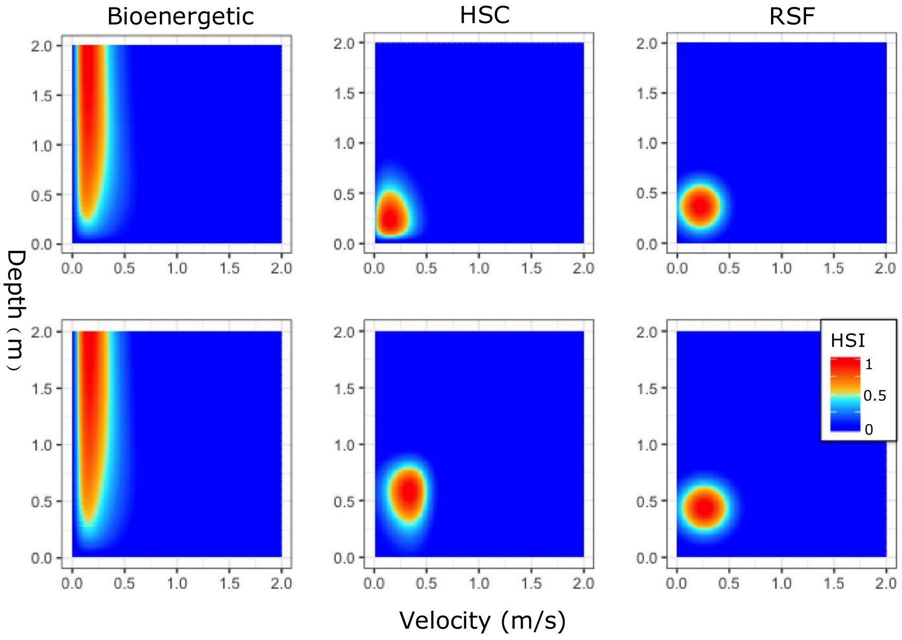

FIGURE 3 Heat maps of standardised habitat suitability predictions across all depth and velocity combinations for each habitat suitability model in the Coquitlam (top row) and Silver Hope (bottom row). HSC, habitat suitability curve; RSF, resource selection function

3 | RESULTS

Although there were broad similarities among habitat suitability estimates among the contrasting models, there were also key differences. The two correlative HSMs were similar, both in terms of their suitability estimates applied to our field data (r = 0.87; Figure 2) and across the entire surface of depth and velocity (Coquitlam: Cramer statistic [C] = 2.29, p = 0.24; Silver Hope: C = 0.73, p = 0.9; Figure 3). These similarities notwithstanding, the HSC model did appear to systematically over-estimate suitability at shallow depths relative to the RSF model (Figure 2). In contrast, correlations between bioenergetic and correlative HSMs were weaker (RSF: r = 0.66, HSC: r = 0.52; Figure 2) and bioenergetic predictions were statistically different from both correlative models in both the Coquitlam (RSF comparison: C = 64.5. p < 0.001; HSC comparison: C = 4.1, p < 0.01) and Silver Hope (RSF comparison: C = 4.1. p < 0.01; HSC comparison: C = 4.0, p < 0.01; Figure 3). Correlative HSMs often predicted higher habitat suitability relative to the bioenergetic HSM (Figure 2); however, they also predicted lower suitability in a large proportion of cases (48% for the HSC model; 41% for the RSF). When we compared suitability surfaces, this divergence was especially evident at greater depths; in general, optimal suitability values for the bioenergetic HSM were shifted to deeper water where the empirical correlative models predicted low to zero suitability (Figure 3).

As expected, the bioenergetic model generally outperformed the correlative models in predicting density and growth, especially for growth, where the bioenergetic HSM explained over 90% of the variation (Figure 4; β = 5.3 [4.7–6.0], R^2 = 0.93). The model predicted suitability values close to 0 for cutthroat parr, all of which

FIGURE 4 Relationships between suitability from bioenergetic and habitat suitability curve (HSC)-based habitat suitability models and cutthroat trout growth. Bioenergetic suitability is standardised relative to mass in order to display the two size classes of fish on the same scale. Error bars represent the standard deviation in growth rates within each enclosure

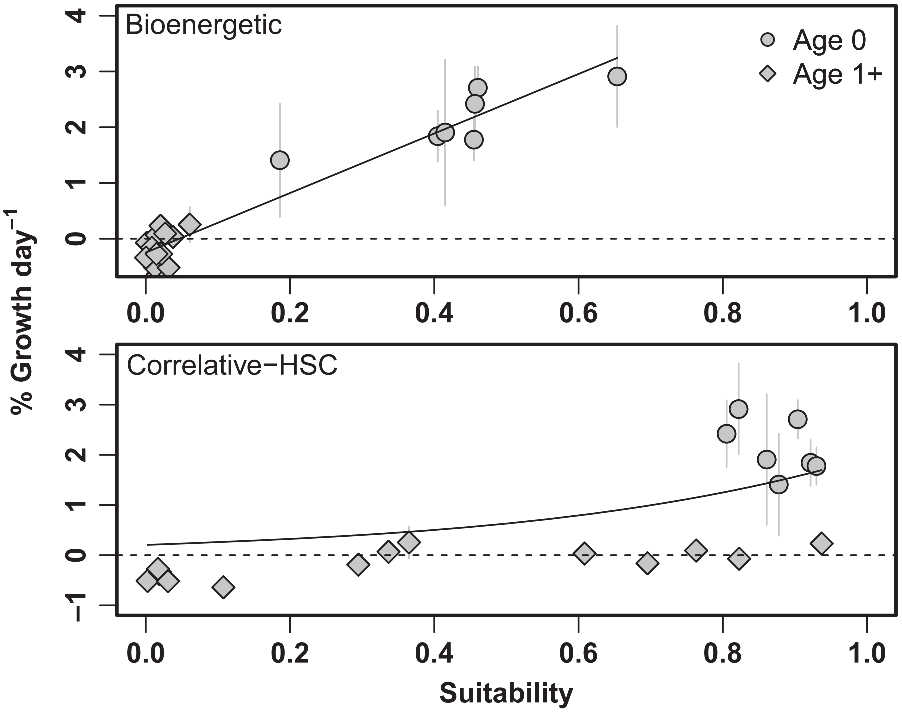

TABLE 3 Results from ordinary least squares regressions relating suitability indices to natural log transformed densities normalised to the mean of each reach

Predictor	Intercept	*B*	Lower CI	Upper CI	R^2
Mean bioenergetic	−1.23	6.00	3.69	8.31	0.38
Mean HSC	−0.95	3.46	1.45	5.47	0.20
Mean RSF	−1.25	4.71	2.81	6.61	0.35
Threshold bioenergetic	−1.42	1.76	0.61	2.91	0.16
Threshold HSC	−1.69	1.65	0.67	2.64	0.19
Threshold RSF	−1.92	1.84	0.83	2.84	0.22

experienced low or negative growth rates during the experiment, while correctly ranking suitability across a broader range of growth rates for young of year (Figure 4). Suitability from the correlative HSC model was also a significant predictor of growth (β = 2.3 [1.3–3.2]), but it explained considerably less variation (R^2 = 0.52; Figure 4) and the strength of the relationship appeared to be driven primarily by the large differences in growth between age classes. For example, the model predicted suitability values ranging from 0 to 0.8 for parr, despite their low growth rates, and predicted high suitability (>0.9) across the range of growth rates for young-of-year.

Mean and above-zero proportional suitability were significant predictors of steelhead density for all three models (Table 3) but there was substantial unexplained variation (Figure 5). When we considered density as a function of the mean suitability value across all points within a channel unit, the bioenergetic model explained the highest proportion of variation (R^2 = 0.38), marginally more than the RSF (R^2 = 0.35), and *c*. 2× more than the HSC model (R^2 = 0.20). The difference between the bioenergetic model and the RSF was magnified when an outlier point with the highest density was removed (Bioenergetic HSM R^2 = 0.38; RSF R^2 = 0.29). All models explained a lower proportion of variation when expressed as the proportion of points with suitability values above 0 (Table 3). Density expressed as g/m^2 exhibited the same patterns as density expressed as fish/m^2 (results omitted for brevity).

4 | DISCUSSION

Bioenergetic and correlative models made divergent predictions of habitat suitability. Both correlative models predicted higher suitability than the bioenergetic HSM in shallow depths and low to intermediate velocities, which is consistent with the idea that displacement of subordinates through territoriality or predation risk could inflate occupancy (and predicted suitability) in energetically unfavourable habitats (assuming minimal benthic or surface feeding). However, the correlative HSMs predicted substantially lower suitability then the bioenergetic model as depth increased, suggesting that steelhead did not use the full range of energetically suitable habitat available to them. This unexpected pattern may also be driven by territoriality if larger conspecifics were excluding fry from deeper habitat (Kaspersson, Höjesjö, & Bohlin, 2012). Alternatively, avoidance of deeper habitats could result from fry minimising predation risk from larger fish or avian predators; for instance, mergansers (*Mergus merganser*) that we frequently observed at the study sites (Dionne & Dodson, 2002).

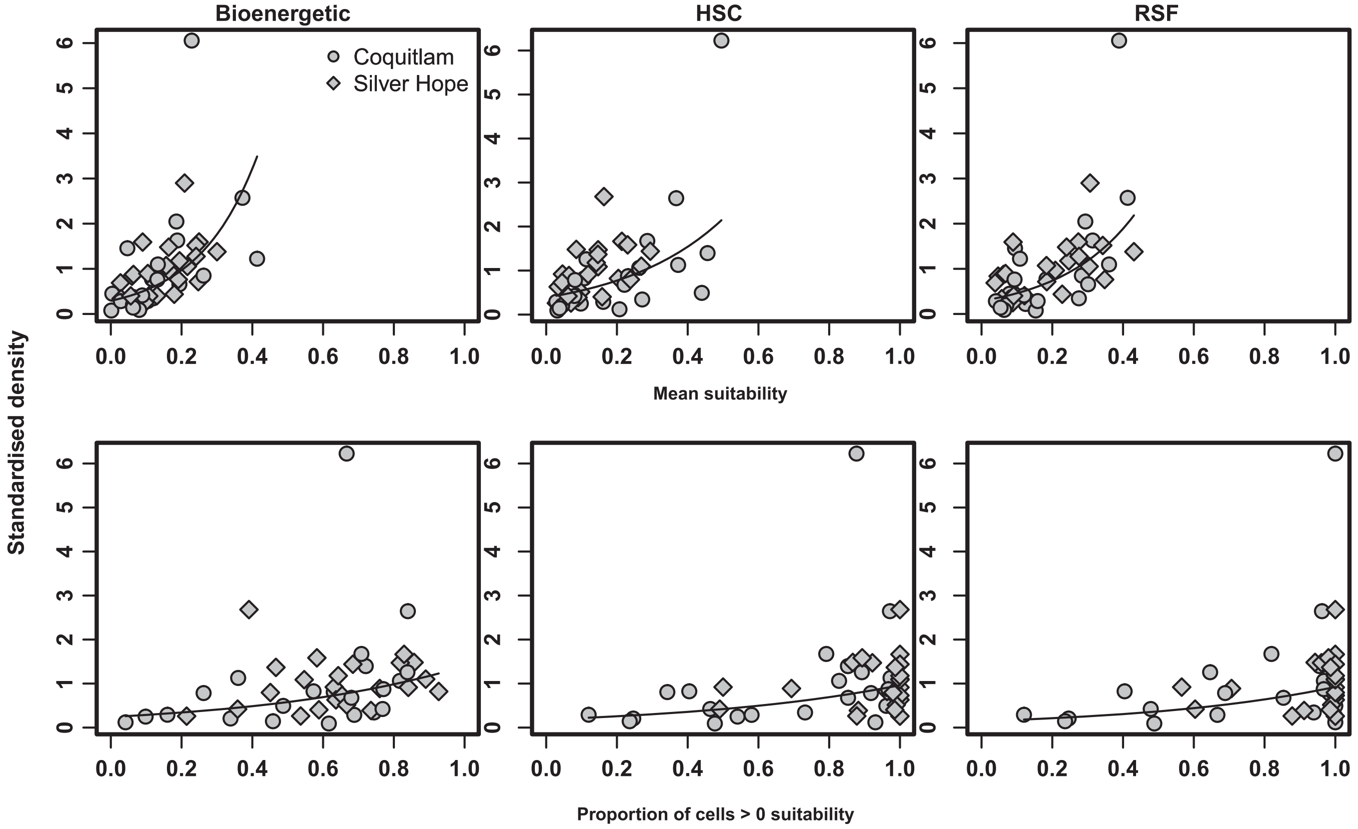

FIGURE 5 Relationships between suitability and density of juvenile steelhead at the channel unit scale. Density (fish/m^2) is standardised relative to the mean of each reach. In the top panels, suitability represents the average of all cells in a channel unit; in the bottom panels, suitability is expressed as the proportion of cells with suitability values greater than zero. Trend lines are from ordinary least squares regressions for each relationship. HSC, habitat suitability curve; RSF, resource selection function

While we cannot disentangle these factors, our results emphasise the diversity of mechanisms that can lead to incongruent suitability estimates between bioenergetic and correlative HSMs. More generally, they highlight the fundamental difference between correlative models that implicitly incorporate biotic interactions, due to their basis on existing distribution, and mechanistic models that are largely independent from biotic interactions due to their basis on the focal organism itself (Buckley, 2008; Kearney, 2006).

When the two correlative HSMs were compared directly, suitability predictions were highly correlated and did not differ statistically across the observed depth and velocity ranges. Several previous comparisons of statistical HSM methods are consistent with this result (Jowett & Davey, 2007; Vadas & Orth, 2001); however, others have found strong differences in suitability predictions when more sophisticated statistical models are used (Beakes et al., 2014; Vismara, Azzellino, Bosi, Crosa, & Gentili, 2001). The extent that habitat suitability estimates differ among contrasting statistical methods is likely to depend on local context; in particular, divergence of univariate and multivariate models is more likely when strong interactions or covariance exist among habitat variables (Schweizer, Borsuk, Jowett, & Reichert, 2007), which was not the case in our system. Despite this broad similarity, the HSC model still systematically over-predicted suitability at shallow depths and explained *c*. 15% less variation in steelhead density relative to the RSF model. These results probably highlight the frequently criticised assumption of independence among habitat variables by univariate HSCs, which is alleviated using multivariate methods.

As expected, bioenergetic HSMs generally outperformed both correlative HSMs at predicting salmonid growth and density, producing an especially striking improvement for cutthroat growth, with the bioenergetic model explaining over 90% of growth variation. Thus, despite our simplifying assumptions relative to other drift-foraging models, e.g. laterally homogeneous velocity and depth through the reaction volume, our model was still able to quantitatively rank habitat quality (as defined by growth rate) with a high degree of accuracy. For the correlative HSM, we cannot discount the possibility that using suitability curves developed outside the study system contributed to the model's weaker predictive power. Therefore, we cannot fully discriminate between inherent biases associated with correlative HSMs and biases introduced from transferring the cutthroat suitability models to novel locations. While this somewhat dilutes the strength of inference from this analysis, the comparison is still meaningful given that transferring suitability curves across systems is common practice (Guay, Boisclair, Leclerc, & Lapointe, 2003). For instance, the HSC for cutthroat fry is used as the standard across the province of British Columbia (R. Ptolomey, personal communication). In addition, the bioenergetic model itself is populated with parameters borrowed from other species and locations, and its robust performance suggests more effective transferability.

Compared with cutthroat trout growth, when predicting steelhead density, the additional explanatory power gained with the bioenergetic HSM was marginal (3–9% relative to the RSF model depending on inclusion of the outlier point). Moreover, while suitability values from all three models were significant predictors of density, over half the variation remained unexplained. This result aligns with the idea that density-independent growth (i.e. in the absence of strong competition or predation risk) is a more direct measure of habitat quality than density (Rosenfeld, 2003). Numerous mechanisms can obscure density-habitat quality relationships (Railsback et al., 2003), which would degrade the predictive power of the bioenergetic HSM. For example, channel units with more energetically profitable habitat may have been under-saturated with steelhead fry due higher predation risk or territorial interactions with larger conspecifics, while channel units with less profitable habitat may have been over-saturated, with many individuals occupying energetically unfavourable habitat as is often observed for juvenile salmonids (Kennedy, Nislow, & Folt, 2008). For the correlative models, these issues should not influence suitability–density relationships in principle, given that biotic interactions are implicitly reflected in realised habitat use (Kearney et al., 2010). Instead, weak relationships may indicate poor transferability across locations (even within the same streams) and spatial scales, e.g. from individual focal points used to generate the models to density in whole channel units. This issue of mixing spatial scales has been a frequent critique of correlative suitability indices for fish (Railsback, 2016) but remains widespread in practice.

The weak ability of models to predict density may also relate to our field methods and the assumptions of the bioenergetic HSM. In particular, our habitat characterisation probably missed important hydraulic features that could influence drift-foraging energetics and/or habitat selection at small scales; for instance, turbulence (Enders, Boisclair, & Roy, 2003) or velocity gradients around flow obstructions (Hayes & Jowett, 1994). These factors were ignored in the simplified drift-foraging model we applied, which assumes that all fish have a laterally homogeneous and symmetric foraging volume. An additional source of error is our assumption that invertebrate drift concentrations and size distributions were constant across depth and velocity gradients in each stream. This assumption is made in nearly all drift-foraging models (except Hayes et al., 2007, 2016) but is at odds with evidence that drift varies spatially with channel hydraulics (Naman, Rosenfeld, Third, & Richardson, 2017; Stark, Shearer, & Hayes, 2002).

In principle, these issues influencing the bioenergetic HSM could be resolved by measuring or simulating the hydraulic environment in more detail and by using a spatially explicit drift-foraging bioenergetics model (e.g. Hayes et al., 2007). However, these more complex models have not consistently predicted density with any more accuracy than our approach (Jenkins & Keeley, 2010; but see Urabe et al., 2010). For example, in one of the most comprehensive drift-foraging model applications to date, Wall et al. (2016) found that net energy intake was a weak predictor of density (R^2 = 0.18) unless an additional model was applied to account for intraspecific competition for drift-feeding territories. These mixed results highlight the likelihood that issues with using density to validate density-independent HSMs may be a primary cause of unexplained variation in our results, as opposed to shortcomings in our methodology. It also highlights the potential value of including biotic interactions in mechanistic HSMs to further improve model predictions and reduce unexplained variation.

4.1 | Management implications

As long as development and human demand for freshwater conflicts with stream fish populations, HSMs will continue to be a necessary tool. Correlative HSMs remain the standard approach but continue to be controversial (Beecher, 2017; Railsback, 2016; Stalnaker, Chisholm, & Paul, 2017), while mechanistic population models have struggled to gain a foothold with practitioners, partly due to their complexity and lack of validation. The bioenergetics-based approach may occupy a useful intermediate niche as it is grounded in the intrinsic energetics underlying habitat use but is still expressed as a simple standardised habitat suitability index that is compatible with existing modelling platforms and the broader hydraulic habitat modelling paradigm currently used by instream flow practitioners.

In addition to the demonstrated improvement in predicting growth and density, bioenergetics-based HSMs provide several other key advantages over correlative approaches. First, because bioenergetic suitability predictions are mechanistic, they should in principle be transferable to novel locations (Buckley et al., 2010; Rosenfeld et al., 2016), whereas correlative HSMs are often strongly dependent on the local conditions where they were developed (e.g. density, prey abundance; Rosenfeld et al., 2005). Second, bioenergetic HSMs are amenable to sensitivity analyses not possible with correlative approaches; for instance, bioenergetic model inputs could be varied to explore the sensitivity of suitability to factors such as temperature or prey abundance that covary with flow and habitat structure (Arismendi, Safeeq, Johnson, Dunham, & Haggerty, 2013; Caldwell, Rossi, Henery, & Chandra, 2018). Third, inclusion of invertebrate drift as an input parameter allows bioenergetic HSMs to capture absolute differences in basal prey production. For instance, while correlative suitability curves assume the same range of suitability (0–1) regardless of productivity, bioenergetic suitability criteria are not constrained to be a standardised (0–1) index; for instance, NEI can be compared directly across streams or flows (Hayes et al., 2016).

Despite these advantages over correlative HSMs, the bioenergetics-based approach is still constrained by some important limitations intrinsic to the PHABSIM framework. Most notably, when converted to a standardised index as presented here the model assigns a single suitability value to a given depth and velocity combination irrespective of adjacent hydraulic conditions; consequently, it cannot account for flow separation near obstructions that allow fish to forage in high velocities while maintaining low swimming costs (Hayes & Jowett, 1994) or larger-scale configurations of mesohabitat patches (e.g. riffles and pools) that influence drift abundance (Naman et al., 2017). In addition, defining suitability as a standardised 0–1 index arguably obscures what the underlying HSM is predicting (e.g. energy gain or occupancy), opening the door for misinterpretation. These issues are largely out of the scope of our study but highlight key points of concern within the broader instream flow modelling paradigm.

Ultimately, practitioners need to weigh the benefits of various HSM approaches with their associated logistical and computational constraints. If fully dynamic predictions of population-level responses to habitat and flow modification are the ultimate objective (Anderson et al., 2006; Lancaster & Downes, 2010), complex mechanistic models offer clear advantages (Ayllón et al., 2016; McHugh et al., 2017; Railsback et al., 2009). However, sufficient information to parameterise and validate these approaches will probably continue to limit their utility in many situations, and their general use in the immediate future. Consequently, simple mechanistic suitability indices, such as the bioenergetics-based approach we have presented, offer a useful avenue to increase the rigor of habitat suitability evaluations within the current instream flow modelling framework. PHABSIM remains the most widely used detailed instream flow modelling application worldwide; consequently, improving the biological realism within PHABSIM may significantly improve the quality of instream flow management decisions.

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DATA ACCESSIBILITY

Data are archived on Figshare. https://doi.org/10.6084/m9.figshare.8148569.

CONFLICT OF INTEREST

There are no conflicts of interest to declare.

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