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ARTICLE

Developing Bioenergetic-Based Habitat Suitability Curves for Instream Flow Models

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Abstract
Instream flow models link a physical habitat model that predicts flow-related changes in hydraulics to a biological model that predicts the response of fish to altered velocity and depth. Habitat suitability curves (HSCs) based on frequency of habitat use (fish occurrence relative to available habitat) remain the most widely used biological models in habitat simulations. However, in some contexts fish density may be a poor indicator of habitat quality, leading to biased predictions of optimal flow. We explore the use of bioenergetics to derive mechanistic HSCs based on the fundamental energetics of habitat use. Using flow-related changes in production of Coho Salmon *Oncorhynchus kisutch* smolt as reference data to evaluate model predictions, we found that bioenergetic-based HSCs matched the validation data better than frequency-based HSCs, which systematically underestimated optimal flows. However, biases remained using bioenergetic HSCs, suggesting that habitat suitability may not be independent of discharge as is often assumed. Declining invertebrate drift concentration, increasing temperature, and density dependence of growth at low flows are potential mechanisms of flow-related declines in habitat suitability; measuring these effects and incorporating them into flow models is an important step in further improving model predictions, particularly at low flows.

Accurately predicting the biological impacts of water withdrawals is becoming increasingly important as human demands for freshwater conflict with flow needs for fish (Poff et al. 2003; Anderson et al. 2006; Arthington 2012). With an increasing global footprint of water withdrawals for irrigation, domestic water supplies, and hydroelectric power generation (Dudgeon et al. 2006), it is critical to have confidence in predictions of biological impact and associated trade-offs among competing water uses. This is especially true for predictions of minimum flow requirements since anthropogenic demands for water are often highest during low flows when stream ecosystems are already stressed, an increasingly common occurrence as climate change exaggerates the severity and duration of drought in many regions (Schindler and Donahue 2006).

Most traditional instream flow models link a physical habitat (hydraulic) model to a biological one (Jowett et al. 2008). The hydraulic model predicts changes in velocity and depth with increasing discharge, and the biological model predicts corresponding changes in habitat area and quality for the target species in response to altered hydraulics. The implicit assumption is usually that the target fish population or life

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stage is habitat limited, so that changes in available habitat match predicted changes in fish abundance (Orth and Maughan 1982). Models like the physical habitat simulation model (PHABSIM) and River2D are the most widely used habitat simulation modeling approaches for predicting biological responses to altered flow regimes (Tharme 2003; Souchon et al. 2008) and are applied worldwide. The main output of PHABSIM is an index of available habitat labeled weighted useable area (WUA), calculated as the product of habitat area and habitat suitability summed across all modeled habitat.

Physical habitat models vary in detail and resolution, ranging from one-dimensional models that only consider changes in velocity parallel to the direction of flow (e.g., PHABSIM) to complex hydraulic models that track velocity vectors in three dimensions. A range of physical models is now available to model hydraulics with varying degrees of accuracy; much of the uncertainty surrounding instream flow predictions now relates to the degree of confidence that the biological model accurately represents habitat quality for the focal fish species (Rosenfeld 2003; Anderson et al. 2006; Ayllón et al. 2012). This is partly due to the challenges in developing simple models that adequately characterize habitat quality for animals (Garshelis 2000; Rosenfeld 2003; Anderson et al. 2006) and partly because hydraulic models are much more easily validated than biological ones. (Note that habitat quality as used throughout this paper refers to any objective metric that is correlated with the fitness consequences of habitat use, such as measured or modeled growth, survival, or fecundity [Railsback et al. 2003; Rosenfeld 2003; Urabe et al. 2010]).

The most common biological models used in flow assessments are habitat suitability curves (HSCs) for velocity, depth, and substrate, which usually represent habitat selection functions based on observed frequency of use of different microhabitats relative to available habitat (Rosenfeld et al. 2005; Ahmadi-Nedushan et al. 2006). Frequency of use of velocity and depth habitat-classes are assessed through field observations (e.g., by snorkeling, electroshocking, etc.), then divided by available habitat and standardized to a maximum of 1 to generate a habitat suitability curve (Jowett et al. 2008; Figure 1). Habitat suitability curves represent a simple but concise biological model of habitat association, which underlies both their widespread appeal and limitations (Mathur et al. 1985; Shirvell 1986). Of particular concern is that frequency of habitat use (or fish density) may not accurately reflect the fitness consequences of habitat use, particularly for territorial species like salmonids where subdominant individuals may be displaced into poor quality habitat at high densities (Van Horne 1983; Baker and Coon 1997; Beecher et al. 2010). Application of a single habitat suitability curve across a range of flows may also be problematic since this assumes that habitat quality is independent of discharge. However, available habitat, fish density, swimming costs, temperature, and prey resources may all vary with discharge, generating poorly understood sensitivity of model outcomes to the assumption that habitat suitability curves are flow invariant (Bult et al. 1999; Holm et al. 2001; Gibson et al. 2008; but see Beecher et al. 1995). There is also a paucity of studies that have validated the biological accuracy of instream flow modeling, i.e., it is rarely demonstrated that predicted changes in available habitat match the population response of fish to altered flows, which undermines confidence in model predictions (Shirvell 1986; Castleberry et al. 1996; Hayes et al. 2012; but see Souchon and Capra 2004).

Despite their shortcomings, frequency-based habitat suitability curves remain the dominant biological model for applications like PHABSIM in most jurisdictions because they are easily generated from field observations and published curves are widely available. In contrast, there has been a proliferation of new approaches for modeling organism distribution and abundance in other disciplines (e.g., Boyce and McDonald 1999; Hughes 2009; Kearney and Porter 2009), including more statistically defendable methods like multivariate logistic regression (Boyce and McDonald 1999; Manly 2002), generalised additive models (Shearer et al. 2015), or multivariate approaches (e.g., Lamouroux et al. 1998; Vismara et al. 2001; Grenouillet et al. 2011). However, all of these models are based on observed frequency of habitat use and are therefore subject to many of the same biases as frequency-based HSCs. Consequently, there has also been a shift from correlative descriptive models to more explicitly mechanistic ones (e.g., Buckley 2008; Buckley and Jetz 2010).

Mechanistic niche models based on the bioenergetics of foraging and organism physiology generate habitat suitability metrics that more directly represent the potential fitness consequences of habitat use (Railsback et al. 2003; Rosenfeld 2003; Kearney et al. 2010). The most detailed mechanistic niche models for fishes have been developed for drift feeders (Hughes and Dill 1990; Guensch et al. 2001; Hughes et al. 2003; Railsback et al. 2009), where habitat suitability is expressed in terms of net energy intake (NEI), the balance between energy gains and energy expenditures in different microhabitats (Hughes and Dill 1990; Baker and Coon 1997). Net energy intake represents the quality of a microhabitat in terms of energy available for growth and reproduction. Although the prediction of growth rates from drift-foraging bioenergetic models are not without error (Hughes et al. 2003; Rosenfeld et al. 2014), estimates of net energy intake are more robust and generally perform well in terms of accurately ranking habitat quality (e.g., Urabe et al. 2010).

Examples of instream flow model validation are rare (where validation means demonstrating that predicted flow effects on available habitat accurately match changes in fish biomass or production; see examples in Souchon and Capra 2004). Beecher et al. (2010) used a data set relating production of Coho Salmon *Oncorhynchus kisutch* smolt to summer low flows to evaluate the accuracy of a PHABSIM model

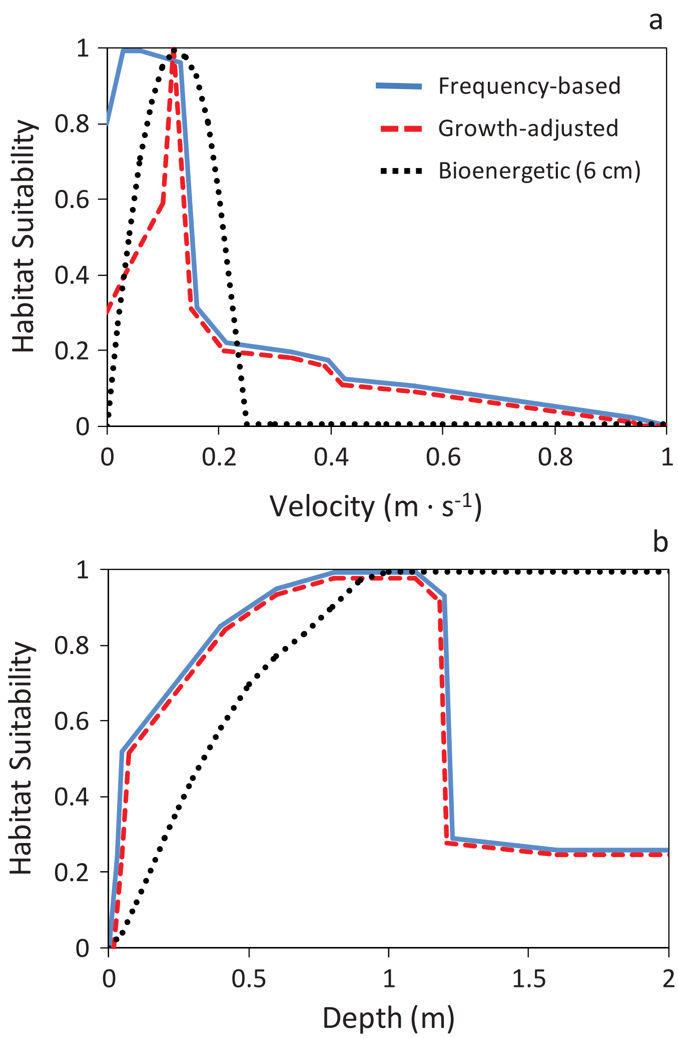

FIGURE 1. Habitat suitability curves (HSCs) for **(a)** velocity and **(b)** depth used for contrasting instream flow modeling scenarios. Solid blue line represents empirical frequency-based HSCs from Beecher et al. (2002), broken red line represents growth-adjusted HSCs, and dotted black line represents bioenergetic-based HSCs for 6-cm-FL juvenile Coho Salmon.

developed for juvenile Coho Salmon rearing flows in Bingham Creek, Washington. Their study demonstrated that frequency-based HSCs greatly overestimated habitat suitability at low stream flow relative to observed low-flow effects on smolt production. In the present study, we use a drift-foraging bioenergetic model to develop bioenergetic-based habitat suitability curves for juvenile Coho Salmon, and compare their performance with the conventional frequency-based HSCs used in Beecher et al. (2010). Our objectives were to (1) use Bingham Creek as a case study to evaluate the performance of mechanistic, niche-based HSCs based on bioenergetics; (2) determine whether bioenergetic-based HSCs have the potential to address biases inherent in frequency-based ones; and (3) evaluate the underlying causation of any observed biases associated with bioenergetic-based HSCs and possible approaches for correcting them. Our overall goal was to develop an accessible alternative to frequency-based habitat suitability curves to improve the level of confidence in predictions from instream flow models, particularly at low flows when fish populations are most sensitive to water withdrawals. While we recognize that PHABSIM applications entail assumptions that are not always biologically realistic (e.g., equal weighting and independence of velocity and depth habitat selection; Mathur et al. 1985; Shirvell 1986), our purpose was neither to defend nor revisit the limitations of PHABSIM, but to test whether the application of bioenergetics within the PHABSIM framework can improve model performance.

METHODS

Study Site and Context

Data used in this study were collected from Bingham Creek in Washington State, a coastal stream tributary to the Satsop River in the foothills of the Olympic Mountains with a drainage area of 82 km^2. Bingham Creek has approximately 25 km of main-stem habitat and a mean flow of ~4.6 m^3/s upstream of the confluence with the Satsop River. Although the watershed has experienced significant historic logging in the past century, it remains 46% forested without significant impacts to instream habitat (Beecher et al. 2010) and produces approximately 1,000 Coho Salmon smolts/km, which is well within the range of expected smolt production for coastal streams (Bradford et al. 1997). The study reach where instream flow modeling was performed was 9 km above the confluence with the Satsop River, averaging a 10.5-m channel width with an upstream basin area of 30 km^2 and a mean flow of approximately 1.7 m^3/s (Beecher et al. 2010). Summer is a time of limited precipitation on the Pacific coast when low flows often extend for 2–3 months between July and September; limited daily flow data for Bingham Creek indicate that a discharge of 0.56 m^3/s was exceeded 90% of the time during the available period of record (1946–1948 and 2001–2004).

Lower velocities and experimental flow reductions are known to reduce prey production from fast water habitats (Stalnaker and Arnette 1976; Harvey et al. 2006), and seasonal flow reductions can create severe resource and habitat limitation for juvenile salmonids, leading to strong density-dependent effects on growth and survival in Pacific coastal streams (Harvey et al. 2005; Grantham et al. 2012). Although higher winter flows may also affect overwinter survival of juvenile salmonids and subsequent year-class strength (Quinn and Peterson 1996), there is little evidence that this is a strong determinant of Coho Salmon smolt production in Bingham Creek.

Coho Salmon in Bingham Creek spawn in the fall, emerge as fry the following spring, rear in the creek as juveniles, and overwinter before smolting to the ocean the following spring.

A smolt trap was operated on Bingham Creek from 1980 to 1992 to monitor spring out-migration of juvenile Coho Salmon smolts as part of a broader monitoring program; only yearling migrants were counted, and production from other potential life history strategies was not included (e.g., fall migrants; Roni et al. 2012). The general impact of summer low flows on juvenile Coho Salmon production can be inferred based on the relationship between total smolt out-migration and low flows the previous summer. This provides an independent validation data set relating low flows to smolt production (Figure 2) that can be used as a benchmark to assess the accuracy of instream flow modeling predictions generated with different types of habitat suitability curves.

Although there is a stream gauge on Bingham Creek, discharge was not recorded between 1980 and 1992 when the smolt trap was in operation. Consequently, Beecher et al. (2010) used the PSSLFI as a metric of relative stream discharge across years (Figure 2); the PSSLFI is based on the sum of the minimum 60-d average daily flows experienced by eight representative Coho Salmon index streams in the Puget Sound region (Zimmerman 2012), and provides an integrated and accurate metric of regional summer precipitation and streamflow (Bingham Creek is directly adjacent to Puget Sound). However, we required actual Bingham Creek flow estimates (in m^3/s) to directly compare observed discharge effects on smolt production with modeled discharge effects using PHABSIM. Flow data for Bingham Creek is not available for the period of measured smolt production; however, daily discharge data is available for the nearby Satsop River for 1980–1992, and for 7 years from 1946–1948 and 2001–2004, when daily discharge was measured in both the Satsop River and Bingham Creek. Bingham and Satsop daily discharges showed a strong positive correlation over the shared 7-year period of record (r = 0.92; n = 2,233; slope = 0.073), which allowed us to estimate Bingham Creek discharge from Satsop River flows, as described below.

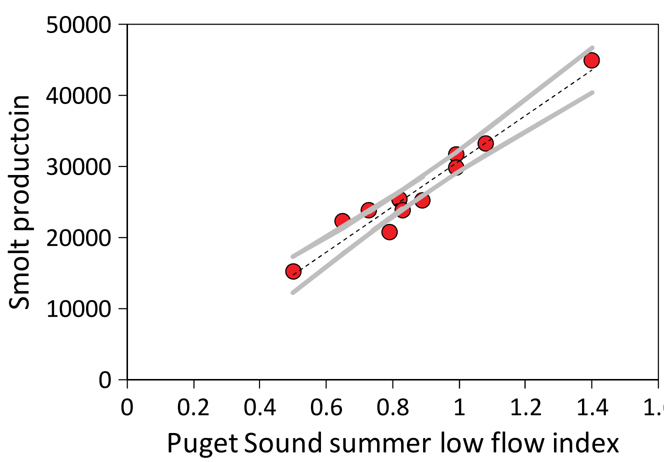

FIGURE 2. Relationship between Coho Salmon smolt production from Bingham Creek (1980–1992) and the Puget Sound Summer low-flow index for the year preceding smolt out-migration. Gray lines represent 95% CIs around the predicted mean.

To characterize interannual variation in low-flow juvenile rearing conditions, we calculated the 60-d summer low-flow discharge for the Satsop River and Bingham Creek as the average of the lowest continuous 60-d discharge in each calendar year, a measure that integrates low-flow conditions over a time scale that is relevant to juvenile growth and survival (e.g., Harvey et al. 2005, 2006). The ratio of Bingham: Satsop 60-d low flow was calculated for the shared period of record (0.079 ± 0.016, 95% CI, n = 7); the missing flow data at the Bingham Creek gauge for the period of smolt production (1980–1992) was then estimated by multiplying Satsop 60-d low flows by the ratio of gauged Bingham: Satsop 60-d low-flow discharges (0.079). A ratio was used rather than a regression of Bingham on Satsop 60-d low flows because of the nonsignificance of both the slope and intercept and the small sample size for comparing 60-d low flows (n = 7).

However, the study site was upstream of the Bingham Creek gauge site and therefore had a smaller drainage area and discharge. We therefore used the ratio of measured low flow at the study site relative to the gauged site to scale flow at the study reach. Sixty-day summer low-flow discharge at the study reach was estimated by adjusting the gauged flows down based on the ratio of the minimum daily flow measured at the study site in September 1996 (an average water year) to the annual minimum daily low flow measured at the downstream gauge between 1946 and 1948, and 2001 and 2004 (0.63 ± 0.2, 95% CI, n = 7, reflecting the smaller drainage area of the upstream study reach). These Bingham Creek low-flow estimates provide a basis for illustrating the application and evaluation of bioenergetic-based HSCs to Bingham Creek; however, their approximate nature introduces uncertainty and therefore necessitates caution when interpreting PHABSIM output relative to the smolt production–low-flow relationship.

Habitat Suitability Curves and Habitat Simulation Modeling Scenarios

We contrasted three different types of habitat suitability curves to assess their performance in predicting flow effects on juvenile Coho Salmon habitat capacity: (1) a traditional frequency-based habitat suitability curve, (2) a frequency-based habitat suitability curve with suitability values adjusted to reflect published relationships between Coho Salmon growth and water velocity, and (3) a bioenergetic-based habitat suitability curve generated using a mechanistic niche model, as described below.

Frequency-based habitat suitability curves.—Data for frequency-based HSCs of depth and velocity were generated using standard instream flow methods (Beecher and Caldwell 2004) during moderate-to-low summer flow conditions in three western Washington streams that included the nearby Satsop River (Beecher et al. 2002). Microhabitat observations of undisturbed fish were collected by carefully snorkeling in an upstream direction and measuring focal depth (to the nearest 1.5 cm) and water column velocity (to the nearest 0.3 cm/s at 60% of total depth); see Beecher et al. (2002) and Beecher and Caldwell (2004) for a detailed description of methods. Microhabitat observations from several streams were combined to generate composite depth and velocity HSCs, which consequently incorporated greater variation associated with differences in habitat selection among streams. Although habitat suitability curves (Figure 1) were not specific to the study reach of Bingham Creek, a direct evaluation of their transferability demonstrated a good correlation (r = 0.85) between joint habitat suitability predicted by the HSCs and observed Coho Salmon density in different velocity–depth bins in Bingham Creek, indicating that HSCs transferred reasonably well between local sites (Beecher et al. 2002, 2010). However, applying HSCs generated in streams of different origin likely contributed to error in the Bingham Creek WUA estimation using frequency-based HSCs.

Growth-adjusted habitat suitability curves.—The frequency-based HSCs for Coho Salmon from Beecher et al. (2002) consistently predicted high habitat suitability at velocities below 12 cm/s (Figure 1a). In part, this reflects the strong preference of juvenile Coho Salmon for pool habitat (Nickelson et al. 1992). However, the observed habitat suitability value of 0.8 at 0 cm/s (where there is no drift flux) is inflated relative to studies that directly measured juvenile Coho Salmon growth at different velocities. Nielsen (1992) observed that nonterritorial (floater) juvenile Coho Salmon experiencing velocities of 2–3 cm/s grew at 39% of the rate of dominant territorial Coho Salmon that fed on drift at average velocities of 11–12 cm/s. Rosenfeld et al. (2005) also observed maximal growth rates of dominant Coho Salmon at 12 cm/s, and growth rates of subdominants close to zero at velocities below 3 cm/s. As is well documented for other taxa (e.g., Garshelis 2000; Van Horne 1983), apparently high suitability (i.e., relative density) in low-velocity microhabitats may be an artifact of competitive displacement of subordinates into poor-quality, low-velocity habitat (Rosenfeld et al. 2005; Beecher et al. 2010), which is most likely to occur at low flows when habitat is most limiting. We therefore created a composite growth-adjusted habitat suitability curve (Figure 1a), where habitat suitability at low velocities was reduced to reflect the large growth differential between 0 and 12 cm/s observed in Nielsen (1992) and Rosenfeld et al. (2005). Habitat suitability values at 0, 3, and 10 cm/s were reduced to 0.3, 0.39, and 0.59 (Figure 1a) based on relative growth rates of 39% and 59% of dominant fish growth at average observed velocities of 3, 10, and 12 cm/s, respectively, from Nielsen (1992). The HSC for depth was not adjusted because frequency-based depth habitat suitability was broadly consistent with observed growth (e.g., Rosenfeld and Boss 2001; Rosenfeld and Taylor 2009).

Bioenergetic-based habitat suitability curves.—The drift-foraging bioenergetic model used to create the bioenergetic-based HSC is described in detail in Rosenfeld and Taylor (2009; also see Rosenfeld and Ptolemy 2012; Rosenfeld et al. 2014). To generate a velocity HSC, the model was used to calculate net energy intake for juvenile Coho Salmon at velocities ranging from 0 to 80 cm/s in 2–10-cm/s increments at a fixed depth value (100 cm), which was not limiting to energy intake (Figure 3). To generate a depth HSC, NEI was estimated in simulations where depth was varied from 0 to 100 cm in 5–10-cm increments at the velocity that maximized energy intake (Figure 3). Each simulation used a

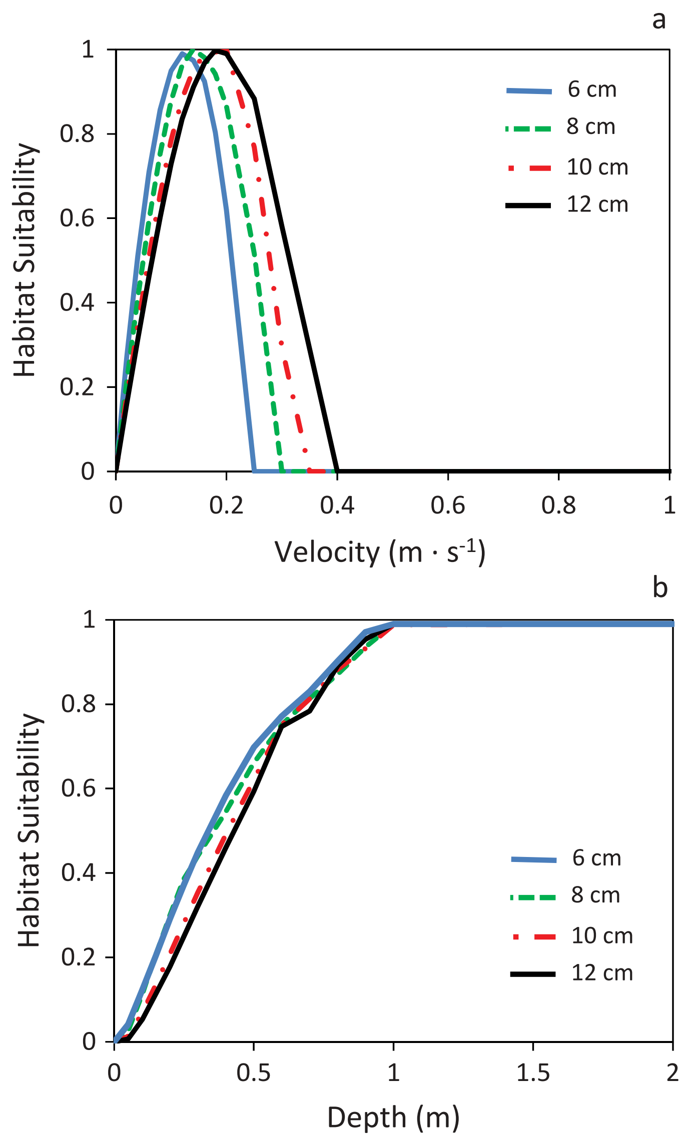

FIGURE 3. Bioenergetic-based habitat suitability curves for **(a)** velocity and **(b)** depth for 6-, 8-, 10-, and 12-cm-FL juvenile Coho Salmon. Solid blue line represents 6-cm Coho Salmon, broken green line represents 8-cm Coho Salmon, the red dash-dot line represents 10-cm Coho Salmon, and the solid black line represents suitability curves for 12-cm Coho Salmon. (See the Appendix for tabular values.)

homogenous velocity and depth field that was wider than the maximum reactive distance of fish to drifting prey.

Habitat quality estimated using a drift-foraging bioenergetic model usually accounts for the effect of variation in depth and velocity adjacent to the focal point (Hughes and Dill 1990) and can also be modified to account for habitat features like the presence of velocity shelters or cover (e.g., Railsback et al. 2003). However, the habitat suitability curve approach eliminates much of this context-specific detail. Generating HSCs assuming a homogenous depth and velocity field, as described above, also ignores the use of velocity shelters by drift-feeding fishes (e.g., Hayes and Jowett 1994), which allows fish to forage in higher-velocity habitats while experiencing relatively low swimming costs. This is a fundamental limitation of the habitat suitability curve approach, which assigns a single habitat suitability value to any given focal velocity or depth regardless of hydraulic context (i.e., adjacent velocity and depth). This simplification is likely of least concern for focal taxa like juvenile Coho Salmon that prefer habitats where velocity gradients are generally low (i.e., pools), and of greatest concern for taxa that use habitats with larger shear velocities (i.e., riffles and runs).

Gross energy intake for every velocity and depth combination was modeled after Hughes and Dill (1990) based on drift concentration in the water column, the size-based reactive distance of fish to three different size-classes of drifting prey (<2.5, 2.5–5.0, and >5.0 mm body length; energy content of 21,790 J/g dry weight), and prey flux through the reactive field, which was a function of water column depth and velocity. Costs of holding at a fixed microhabitat velocity were modeled using the generic swimming cost function for Sockeye Salmon *O. nerka* in the original Hughes and Dill (1990) drift-foraging model, and the incrementally higher costs of prey interception from a central foraging focal point based on maximal swimming costs of Brown Trout *Salmo trutta* (after Hayes et al. 2000; Hughes et al. 2003). Net energy intake was calculated as gross energy intake less swimming costs, including standard metabolism (Hughes and Dill 1990). (Readers are referred to Rosenfeld and Taylor 2009 and Rosenfeld et al. 2014 for a more complete model description.) Focal depths of fish were assumed to be 40% of the water column depth, which is appropriate for juvenile Coho Salmon which typically hold in the water column of pool habitats (Nickelson et al. 1992; Beecher et al. 2002). Invertebrate drift concentrations were not available for Bingham Creek, and we substituted daytime invertebrate drift values measured in pools and riffles during summer low flow in Husdon Creek, a coastal stream on the Sunshine Coast of British Columbia that also supports juvenile Coho Salmon and anadromous Cutthroat Trout *O. clarkii* (Rosenfeld and Boss 2001). While borrowing this parameter from another stream is a potential source of error as absolute NEI will be sensitive to drift concentration, standardizing NEI to a maximum of 1 (see below) should help normalize NEI as a relative rather than absolute estimate of habitat quality.

Net energy intake was modeled assuming a juvenile Coho Salmon FL of 6 cm and weight of 2.5 g, which is a typical size for juvenile Coho Salmon in late summer–early fall in coastal streams, including Bingham Creek. To understand how fish size affects the shapes of bioenergetic-based habitat suitability curves and corresponding optimal flow predictions, we also generated habitat suitability curves for 8, 10, and 12-cm-FL Coho Salmon, with average weights of 6.1, 12.1, and 21.2 g, respectively (Figure 3). Temperature data over the sampling period were not available for Bingham Creek. Consequently, modeling scenarios were run at a fixed temperature of 12°C, which is typical of average late summer–early fall temperatures in many coastal streams. Exploring the sensitivity of bioenergetics-based habitat suitability curves to temperature and drift was beyond the scope of this case study, which focuses on demonstrating the concept and approach, but a formal sensitivity analysis would be important for the further development and application of bioenergetic-based HSCs.

Physical Habitat Simulation Modeling

Cross-sectional data for instream flow modeling was collected in 1996 at nine permanent transects, which is a typical degree of replication for instream flow studies (Payne et al. 2004), particularly for relatively homogenous streams like Bingham Creek, although it is a lower number than is ideal for representing available habitat with a very high degree of confidence. Transects were established in representative habitat types in the study reach, where bed elevation, depth, and velocity were measured at calibration flows of 0.3, 1.0, and 1.8 m^3/s. Data were collected following standard instream flow procedures and protocols as described in Beecher and Caldwell (2004), entered into the PHABSIM modeling platform, and modeled according to standards outlined in Beecher et al. (2010). Simulated velocities, depths, and habitat suitabilities were modeled using a log-log discharge rating and water velocity regression procedure (IFG4) over a discharge range from 0.14 to 2.3 m^3/s in 0.14-m^3/s increments (5–80 ft^3/s in 5-ft^3/s intervals). Measured velocities ranged from –4 to 59 cm/s at low discharge and –23 to 128 cm/s at high discharge. Mean and median deviations between modeled and observed velocities averaged for all sections across all three calibration flows were 2.3 and 0.9 cm/s, respectively. Deviation of modeled water surface elevations from observed elevations at calibration flows averaged 0.5 cm, with a median deviation of 0.3 cm.

Modeling flow-related changes in habitat suitability.—Most instream flow applications use a single habitat suitability curve for depth or velocity across a range of discharges. The implicit assumption is that the habitat quality associated with a specific depth or velocity value is independent of flow across the simulated flow range. Although this assumption has been supported in some ecological contexts (e.g., Beecher et al. 1995), as flows decline and habitat area shrinks greater density-dependent competition for resources may lead to decreased per capita resource availability and therefore lower habitat suitability (Kramer et al. 1997). Similarly, invertebrate drift is qualitatively known to decline seasonally as flows decrease (Romaniszyn et al. 2007; Leeseberg and Keeley 2014), although the opposite pattern has also been observed (e.g., see Wooster et al. 2016), potentially contributing to declining habitat quality with reduced discharge. Capturing declining habitat quality in a traditional instream flow modeling framework would require a series of habitat suitability curves of declining maximum value, or an empirical function to reduce the maximum value of suitability curves at lower flows.

One approach for empirically relating habitat quality to discharge is to use the *P*-parameter in the Wisconsin bioenergetics model (Hewett and Johnson 1992), which estimates daily consumption by fish as a proportion of satiation ration. Based on fish length, weight, and temperature, the Wisconsin model can be used to back-calculate the proportion of satiation that a fish must have experienced to achieve observed growth, and *P*-values can then be related to environmental parameters. For example, *P* has been shown to correlate strongly with invertebrate drift concentration across a set of Rainbow Trout *O. mykiss* streams (Weber et al. 2014). Railsback and Rose (1999) also showed that temperature-standardized *P* for juvenile Rainbow Trout systematically declined with stream discharge across a set of six trout streams in the Sierra Nevada of California, most likely as a result of declining invertebrate drift, increasing fish density at low flows, or both.

To test whether including declining habitat quality at reduced flow improved the accuracy of minimum instream flow predictions for juvenile Coho Salmon in Bingham Creek, we used the Railsback and Rose (1999) empirical relationship between juvenile trout *P* and discharge to reduce habitat suitability values with decreasing flow. After Railsback and Rose (1999), we modeled average *P* as a function of log specific discharge (Figure 4a), where specific discharge is discharge per meter of channel width (i.e., total stream discharge divided by channel width); specific discharge facilitates comparisons across streams by correcting for effects of channel size. In order to make changes in *P* more directly comparable to NEI, we subtracted the estimated maintenance ration for juvenile Coho Salmon (P = 0.2, from Everson 1973 and Corey et al. 1983) from the *P* versus specific discharge relationship to generate the balance of energy intake available for growth ($P\text{-}P_{\text{maint}}$; Figure 4b). This value was then converted to a proportional reduction in net *P* by dividing by the asymptotic value of maximum observed $P\text{-}P_{\text{maint}}$ at 0.09 m^3/s (Figure 4c). This provides an empirical relationship for adjusting HSCs as a function of discharge (Figure 4c, inset); its application needs to be tempered by the typical caveats associated with extrapolating relationships between species and streams. Ultimately, the transferability of this relationship across streams will depend on how generalizable the mechanisms are linking decreasing habitat quality and flow and how sensitive these relationships are to local conditions of temperature or drift concentration, which has yet to be determined. However, our primary goals here were to (1) evaluate whether this method can serve as a practical approach for modeling flow effects on habitat quality, (2) evaluate whether the Bingham Creek example supports the inference that habitat quality is flow dependent, and (3) determine whether accounting for flow-related declines in habitat suitability improves model fit.

Comparison of modeling scenarios.—Model fit was assessed for the three different HSCs (frequency based, growth adjusted, and bioenergetic), for the bioenergetic HSC following the inclusion of flow-related declines in habitat suitability, and finally for the four different sizes of Coho Salmon (6, 8, 10, and 12-cm FL) using bioenergetic HSCs, including flow-related decline in habitat suitability. Model fit was evaluated by (1) superimposing plots of reach scale WUA versus discharge over the smolt production versus discharge relationship for Bingham Creek, and (2) directly comparing slopes, intercepts, and root mean square error (RMSE) of models to the benchmark smolt production versus discharge relationship for flows between 0.14 and 0.28 m^3/s. Discharges that maximized WUA were also compared with the flow that maximized smolt production. Flows at maximum WUA were compared with the lower 95% CI of peak smolt production. The 95% CIs on the relationship between Bingham Creek discharge and smolt production include uncertainty in the flow conversion ratios, i.e., CIs were generated using the 95% confidence values of conversion ratios. We focused only on model fit at low flows since summer low flow was the limiting habitat bottleneck of interest and improved prediction of biological response at low discharge was the primary objective. It should be noted that this approach assumes that the observed maximum discharge and smolt out-migration in our 11-year time series represents the flow that maximizes smolt production. It is possible that the flow that maximizes smolt production actually occurs at a higher discharge beyond the range of our data set, or beyond the range of observed summer low flows in Bingham Creek; a longer reference data set of smolt production across a wider range of discharges, demonstrating a distinct asymptote or decline at higher flows, would be ideal.

Because maximum reach-scale WUA differs considerably among the frequency, growth-adjusted, and bioenergetic PHABSIM simulations, WUA versus discharge relationships were standardized to a maximum of 1 by dividing WUA by the maximum WUA value in each simulation. The smolt production versus discharge relationship was also standardized to a maximum of 1 by dividing by maximum smolt production in the time series. Standardizing WUA curves in instream flow management is common when assessing optimal flows (e.g., Goater et al. 2007; Ahmadi-Nedushan et al. 2008; Ayllon et al. 2012; Wilding et al. 2014), as it is generally the shape of the

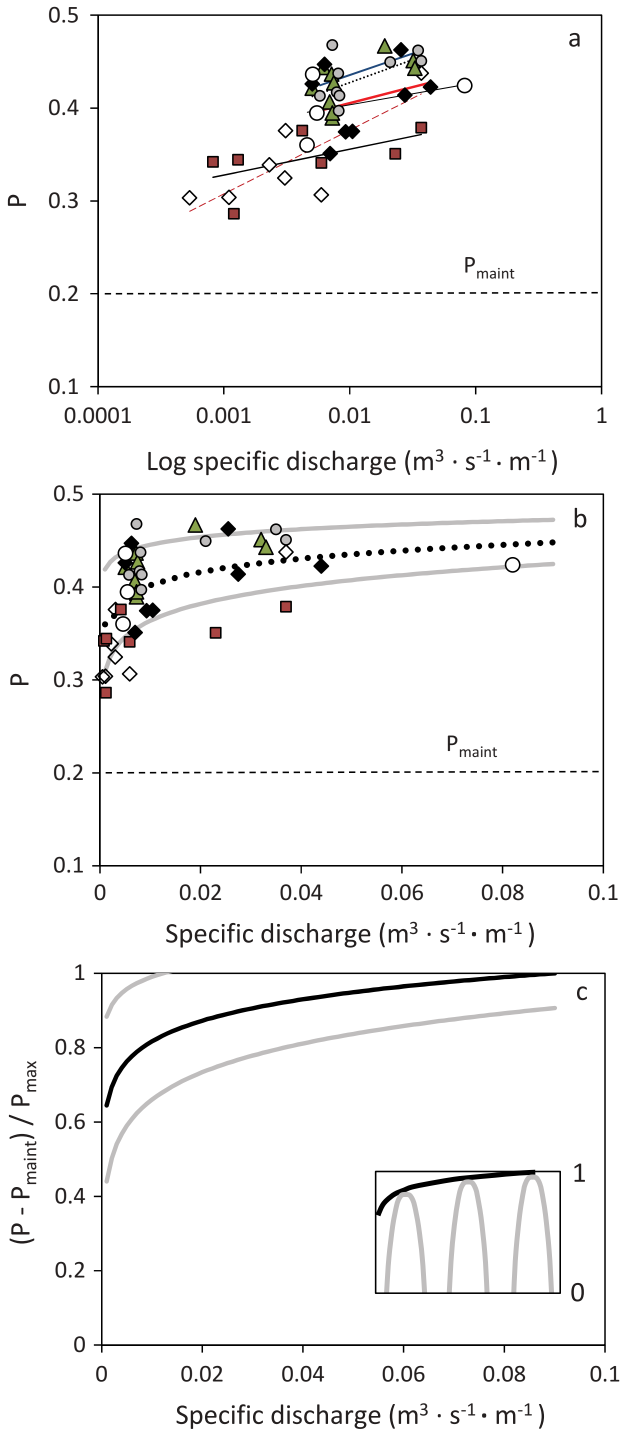

FIGURE 4. **(a)** Relationship between P (ration as a proportion of satiation) and log specific discharge from six Rainbow Trout streams in California (data from Railsback and Rose 1999), where different symbols and associated lines represent separate streams sampled across multiple flows, and horizontal broken line represents approximate maintenance P; **(b)** the same function as in (a) expressed on an arithmetic x-axis scale to highlight the nonlinearity; and **(c)** expressed as consumption in excess of maintenance (P-P_{maint}) standardized to a maximum of one. Inset in (c) is for illustrative purposes and visualizes the reduction in maximum value of the habitat suitability curve with discharge; gray lines represent 95% CIs.

curve (i.e., flow-related trends in WUA) that is of interest rather than the absolute scaling of WUA, which depends on reach length and channel width. Maximum WUA among other simulations showed little variation and was therefore not standardized in illustrations.

Weighted useable area model fit (in terms of RMSE) was estimated for each standardized WUA versus discharge scenario based on the difference between predicted standardized WUA and standardized smolt production at each of the annual low-flow discharge values associated with the 11 smolt production estimates. The RMSE of the difference between predicted relative WUA and relative smolt production (each on a 0–1 scale) was calculated as a quantitative measure of relative model fit for each scenario.

RESULTS

There was a strong positive relationship between PSSLFI and smolt production (Figure 2; smolts = 32,044·PSSLFI – 1,250; $r^2 = 0.95$, $p < 0.0001$). This relationship was linear and did not show a threshold flow beyond which smolt production declined steeply, possibly because observed summer low flows had a limited range. The relationship between smolt production and estimated Bingham Creek discharge was similar but more variable ($r^2 = 0.64$, $P < 0.003$), likely reflecting error in Satsop versus Bingham flow estimates associated with the limited available gauging data. This also was reflected in the wider 95% CIs around the smolt production–discharge relationship, which nevertheless had a significantly positive slope (95% CI, 25,000–202,000 smolts/m^{-3}·s^{-1}; Figure 5). It should be noted that these broad 95% CIs also include uncertainty in the calibration of study site discharge against Satsop River flows and the downstream Bingham gauge.

Superimposition of the frequency-based, growth-adjusted, and bioenergetic-based HSCs for 6-cm Coho Salmon highlights their differences (Figure 1). The bioenergetic-based HSC predicts zero habitat suitability (NEI) at velocities in excess of 25 cm/s, when swimming costs exceed energy intake, and at zero velocity, when the model by default predicts no drift flux past the fish. The bioenergetic HSC may underestimate habitat suitability at higher velocities if hydraulic refuges are available that allow fish to hold at lower velocities than the average of the vertical velocity profile (Hayes and Jowett 1994; Railsback et al. 2003; Hafs et al. 2014). The bioenergetic model also likely underestimates habitat quality at zero velocity since fish can feed on terrestrial or benthic invertebrates in still water (Nielsen 1992; Harvey and Railsback 2014). In contrast, relative to the bioenergetic-based HSC, the frequency-based HSC predicts very high habitat suitability values at low velocities including 0 cm/s, similar to frequency-based HSCs for juvenile Coho Salmon reported elsewhere (e.g., Hampton 1988; but see Bovee 1978). The frequency-based HSC also predicts positive (but low) habitat suitability at higher velocities, suggesting some use

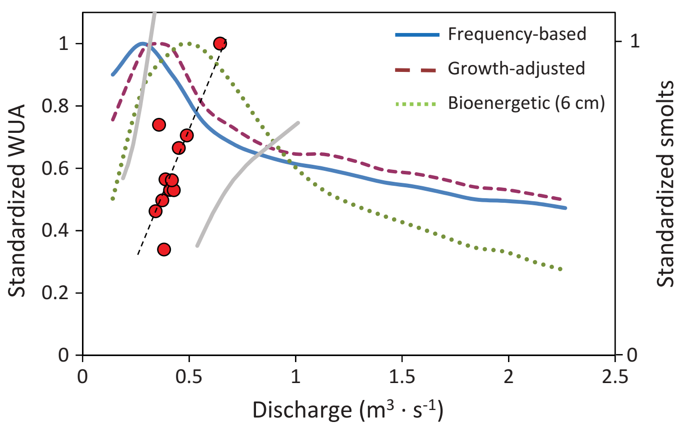

FIGURE 5. Changes in standardized weighted useable area (WUA; standardized to a maximum of 1) with discharge estimated for Bingham Creek using the frequency-based habitat suitability curve (HSC; solid blue line), the growth-adjusted HSC (broken red line), and the bioenergetic-based HSC for 6-cm Coho Salmon (dotted green line). Red circles represent observed smolt production (standardized to a maximum of 1) plotted against summer low-flow discharge. Broken black line represents the predicted mean smolt production, gray lines represent 95% CIs.

of velocity refuges by fish in microhabitats with higher average water column velocities. The growth-adjusted HSC shares a peak habitat suitability of 12 cm/s with the bioenergetic-based HSC, and more realistically predicts positive (but lower) habitat suitability at zero velocity. The bioenergetic-based habitat suitability curve also shows a relatively monotonic increase in habitat suitability with depth with an asymptote near 1 m, whereas the frequency-based HSC based on microhabitat observations shows a sharp decline at 1.2 m depth, perhaps reflecting increased predation risk from trout in deeper pools, or this could simply be an artifact of a low frequency of microhabitat observations at greater depth.

The habitat suitability curves for 8, 10, and 12-cm juvenile Coho Salmon have similar shapes but show a progressive shift to higher velocities (Figure 3a), reflecting the enhanced swimming abilities of larger fish and their greater capture success and reactive distance at higher velocities (Hill and Grossman 1993; Rosenfeld and Taylor 2009).

As observed by Railsback and Rose (1999), there is a significant positive relationship between *P*, the proportion of maximum consumption for juvenile Rainbow Trout predicted by the Wisconsin bioenergetics model, and specific discharge (Figure 4a), with an asymptote between 0.08 and 0.01 $m^{-3} \cdot s^{-1}$ per meter width of stream channel (Figure 4b). Expressing this in terms of a relative decrease in average NEI (Figure 4c) generates a function where energy in excess of maintenance costs decreases approximately 35% as specific discharge declines from 0.09 to 0 $m^{-3} \cdot s^{-1}$ per meter of channel width.

Weighted useable area modeled using the frequency-based HSCs predicted increased available habitat as flows declined, an opposite trend to the actual observed low-flow effects on smolt production (Figure 5) as noted in Beecher et al. (2010). Although WUA from the frequency-based habitat suitability curve predicts a slight decline at very low discharge, the predicted optimal flows were below those associated with maximum smolt production. Thus, the frequency-based HSC failed to reproduce the general effects of decreasing flows on smolt production or to accurately identify the discharge that maximizes WUA, which falls outside of the lower 95% CI for the smolt production–discharge relationship. However, the model fit for the frequency-based HSC in terms of RMSE was comparable to the growth-adjusted or bioenergetic-based HSCs (Table 1), although this likely reflects the overall poor statistical fit of all three models.

The growth-adjusted HSC performed somewhat better (Figure 5), i.e., predicted optimal flow is shifted to a somewhat higher discharge within the lower 95% CI based on smolt production, but the decline in WUA at low flows remains small and the model fit remains poor.

Trends in WUA predicted using the bioenergetic-based HSC for 6-cm Coho Salmon match flow-related declines in smolt production better than either the frequency-based or growth-adjusted curves; the predicted optimal discharge was well within the 95% lower CI for the smolt production–discharge relationship, and only the bioenergetics-based HSC produced a large drop in available habitat comparable to the decline in smolt production at low flows. However, this drop (the declining leg of the WUA–discharge relationship) occurred outside of the 95% CIs for smolt production (Figure 5), resulting in the poor statistical model fit (RMSE). Thus, despite providing a more accurate overall picture of how available habitat changes as flows decline, the bioenergetic-based HSC still overpredicted available habitat at low flows; this suggests

TABLE 1. Regression parameters and root mean square error (RMSE) for plots of weighted useable area as a function of discharge generated with different habitat suitability curves (HSCs), as illustrated in Figures 5 and 6. Slope represents the slope of the descending limb of the weighted useable area versus discharge curve at the lowest flows (between 0.14 and 0.28 m^3/s). Intercept represents the *y*-intercept of the extrapolation of the slope between 0.14 and 0.28 m^3/s. The first line of the table (labeled "smolt production") represents the slope and intercept of the relationship between smolt production and discharge (the validation data set).

HSC simulation	Slope	Intercept	RMSE
Smolt production	1.7	–0.11	
Frequency based	0.7	0.80	0.38
Growth adjusted	1.7	0.51	0.43
Bioenergetic (6 cm)	2.5	0.15	0.40
Bioenergetic with drift reduction at low flow			
6 cm	2.6	0.08	0.40
8 cm	2.4	0.02	0.32
10 cm	2.1	–0.04	0.22
12 cm	1.9	–0.04	0.16

that habitat quality may decline more quickly with decreasing flows than predicted using the bioenergetic-based HSC, although calibration of other model parameters may also be in error.

Including flow-related declines in habitat suitability using the *P* versus specific discharge relationship shifted the WUA curve inside the 95% CIs for smolt production (Figure 6a); however, this incremental improvement was minor compared with shifting from a frequency-based to bioenergetic-based HSC approach. Bioenergetic-based HSCs for progressively larger juvenile Coho Salmon generated trends in WUA that more closely matched the smolt production–discharge relationship (Figure 6b; Table 1).

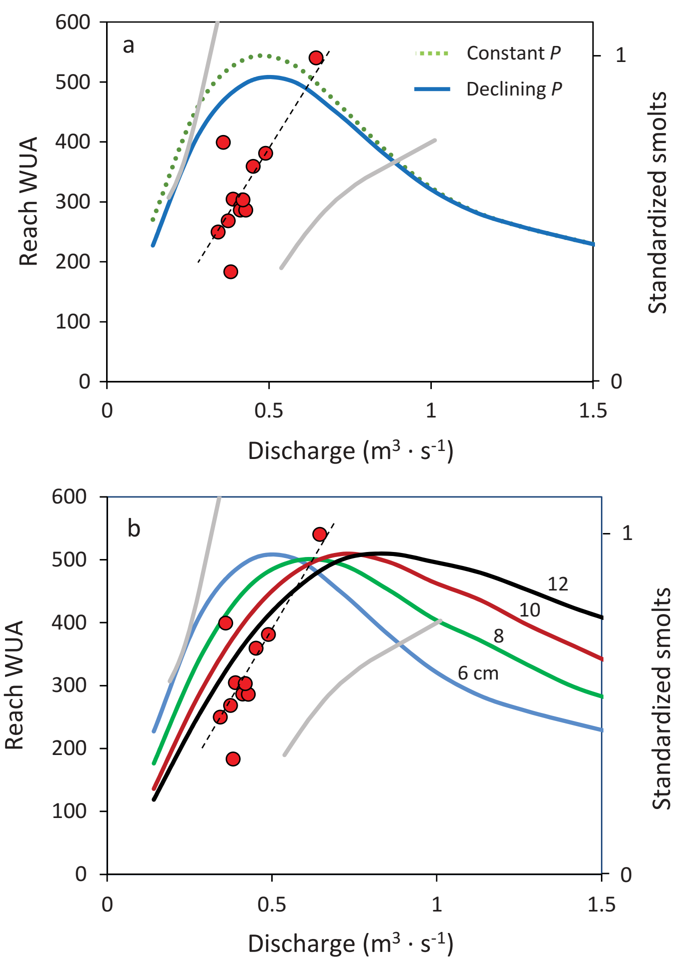

FIGURE 6. **(a)** Trends in reach-scale weighted useable area (WUA) with discharge estimated for Bingham Creek using the bioenergetic-based habitat suitability curve for 6-cm Coho Salmon assuming constant invertebrate drift (dotted green line), and assuming that maximum habitat suitability declines with *P* as illustrated in Figure 4c. **(b)** Trends in WUA with discharge using bioenergetic-based habitat suitability curves for 6, 8, 10, and 12-cm juvenile Coho Salmon, modeled assuming that maximum habitat suitability declines with *P*. Red circles represent observed Coho Salmon smolt production (standardized to a maximum of 540 to match reach-scale WUA) plotted against summer low-flow discharge. Broken black line represents the predicted mean smolt production, gray lines represent 95% CIs.

DISCUSSION

Bioenergetic-based HSCs applied to Bingham Creek performed better than frequency-based HSCs in terms of predicting changes in available habitat that match observed flow effects on smolt production, although the strength of this inference needs to be tempered by the considerable uncertainty in our discharge–smolt production relationship. Many earlier studies have shown that instream flow predictions are sensitive to the shape of the habitat suitability curve (e.g., Ayllón et al. 2012; Rosenfeld and Ptolemy 2012); this study and Beecher et al. (2010), however, specifically highlight the potential for frequency-based HSCs to systematically overestimate habitat quality at low velocities and flows. The potential for this bias may be driven by territorial behavior that causes subordinate individuals to use poor-quality habitat at high densities, declining habitat quality at low flows, or both. In general, because subdominant individuals are more likely to be displaced into slow-velocity habitats where energy expenditures are low (Nielsen 1992; Baker and Coon 1997), territoriality is most likely to inflate the value of lower velocity habitats. This potential bias may be a general concern for territorial species where dominant individuals displace subordinates to low-quality habitat at high density, which includes the juveniles (and to a lesser extent adults) of many species of salmonid. Similarly, if reduced habitat quality with declining flows is a general feature of flowing waters, then application of a single HSC across all discharges may also inflate habitat quality at low flows, raising concern that a bias towards underestimating optimal flows could manifest in many flow assessments.

The assumption that habitat quality is flow invariant (e.g., Holm et al. 2001) remains a key shortcoming of traditional PHABSIM modeling. Support for this assumption has been demonstrated in some ecological contexts; for example, Beecher et al. (1995) found that HSCs for steelhead (anadromous Rainbow Trout) parr at low densities performed well across a range of flows. However, while the potential flow dependence of habitat quality is widely recognized (e.g., Hayes et al. 2012, 2016), it remains broadly ignored in most instream flow modeling applications. The paucity of instream flow studies that evaluate PHABSIM predictions against independent measures of fish production makes it difficult to assess whether this simplification is consequential or not. Evidence for flow-related declines in drift (e.g., Romaniszyn et al. 2007; Leeseberg and Keeley 2014), reduction in ration (*P*; Railsback and Rose 1999), and elevation of temperature (Arismendi et al. 2013) suggests that it may be. We demonstrate a relatively simple method of modeling flow-related declines in habitat quality using an empirical function that scales maximum habitat quality (*P*) with flow. A less-generic approach would be to directly input declining drift concentrations into a drift-foraging model (e.g., Hayes et al. 2016). A thorough assessment of flow-related trends in habitat quality (in terms of *P*, invertebrate drift, or fish growth and survival) is needed to assess whether there is a credible basis for adjusting habitat suitability curves with discharge and for evaluating how generalizable any such relationships might be.

This study is one of a growing number that supports the value of mechanistic niche models over correlative ones in instream flow applications (Railsback et al. 2003; Urabe et al. 2010; Hayes et al. 2012). Several earlier studies have also generated bioenergetic-based HSCs for salmonids (Baker and Coon 1997, Brook Trout *Salvelinus fontinalis*; Jowett et al. 2008, Brown Trout). Although these studies did not evaluate model performance in terms of predicted fish production, they showed that bioenergetic-based HSCs broadly matched frequency-based ones. We extend these results by showing that bioenergetics-based HSCs were successful in minimizing the apparent biases potentially associated with frequency-based HSCs in Bingham Creek, and their improved performance is consistent with the growing use of mechanistic niche models for other taxa (Kearney and Porter 2009; Monahan 2009; Buckley and Jetz 2010). However, this conclusion also needs to be tempered by the approximate nature of our discharge estimates for Bingham Creek, as well as uncertainty in the discharge that maximizes smolt production because of the relatively narrow range of flows in our smolt production time series, and further validation of the bioenergetic-based HSCs approach is clearly warranted.

The use of bioenergetic-based HSCs to represent habitat quality may offer additional advantages over frequency-based ones. First, habitat selection by animals varies with density (Kramer et al. 1997), so that observations collected from the same stream at different densities will generate different frequency-based HSCs, even when intrinsic habitat quality is constant. In contrast, predictions from our drift-foraging bioenergetic model are density independent, i.e., NEI was estimated in the absence of competition, which should, in principle, bring a greater measure of objectivity to the assessment of habitat suitability and enhance transferability of HSCs among streams. Second, although temperature was held constant when generating HSCs in this study, temperature could also be varied to create a family of HSCs for assessing the joint effects of changes in temperature and discharge. This would be especially relevant to instream flow modeling since deceased flows are often associated with elevated temperatures (Arismendi et al. 2013), although it remains to be demonstrated that a simple bioenergetic-based HSC approach as presented here produces projections equivalent to population-level demographic models. Third, flows that maximize available habitat based on frequency-based habitat suitability curves do not necessarily maximize production and delivery of invertebrate prey to drift-feeding fishes (Rosenfeld and Ptolemy 2012). In contrast, bioenergetic-based habitat suitability curves maximize NEI and therefore energy flux to the target fish population.

Because drift-foraging models incorporate the allometry of body size, generating HSCs to model size-related differences in response to flow is also straightforward (e.g., Baker and Coon 1997). In our Bingham Creek example, modeled flow effects on available habitat for larger Coho Salmon fall within the 95% CIs for the discharge–smolt production relationship, suggesting that low-flow effects on larger juveniles may have a disproportionate influence on smolt production the following spring, which is consistent with the higher overwinter survival of larger juvenile Coho Salmon (Quinn and Peterson 1996). However, the strength of this apparent pattern should not be overinterpreted, since systematically varying any parameter will often improve model fit.

Despite their advantages, mechanistic niche models are not always superior to correlative ones (e.g., Nabout et al. 2012), and the limitations of bioenergetic-based HSCs need to be recognized. These include failing to account for the effects of predation risk or competing species on habitat quality, factors that are well integrated into correlative HSCs based on observed habitat use of wild fish. Swimming costs were also modeled assuming a homogenous vertical velocity profile with no flow refugia (e.g., boulders or other habitat structure). Despite these simplifications, the bioenergetic-based HSCs outperformed the frequency-based ones in our Bingham Creek application, suggesting that the effects of predation, competition, and velocity refuges on juvenile Coho Salmon habitat selection may be small relative to the effects of modeled NEI. Habitat suitability curves based on NEI alone can also be adjusted to include distance to cover from predation or the effects of velocity refuges, which can be modeled by simply reducing swimming costs in habitat where velocity refuges are present (e.g., Railsback et al. 2003).

While we advocate for the further development of bioenergetic-based HSCs in flow modeling, they should not be viewed as an exclusive substitute for frequency-based HSCs. Rather, bioenergetic-based HSCs represent complementary biological models that can provide evidence for accepting or rejecting standard frequency-based HSCs. However, because bioenergetic-based HSCs are inherently mechanistic, our case study suggests that the use of generic bioenergetic-based HSCs may minimize the potential for bias when drift-feeding fish are known to be territorial and prefer low-velocity pool habitats. Although the positive performance of bioenergetic-based HSCs in Bingham Creek is encouraging, despite the simplified parameter assumptions with respect to temperature and drift concentration, a more rigorous validation of bioenergetics-based HSCs is clearly needed, in particular a robust assessment of sensitivity to varying drift and temperature.

One of the key conclusions from this study and Beecher et al. (2010) is the importance of evaluating predictions from competing instream flow models against direct measures of flow effects on fish production. Given the widespread application of PHABSIM methodologies, independent assessments of instream flow modeling predictions remain surprisingly rare (but see Irvine et al. 1987; Souchon and Capra 2004; Moir et al. 2005; Ovidio et al. 2008; Bradford et al. 2011). Although the quality of the instream flow data for Bingham Creek and the short length of our smolt production time series limit the strength of inference that can be drawn from our case study, it nevertheless illustrates an accessible approach for model validation.

Anderson et al. (2006) emphasized the need for the biological component of instream flow models to move beyond environmental tolerances to include flow effects on consumer resource dynamics. Habitat suitability curves based on drift-foraging bioenergetics represent a step in this direction because they account for the effects of both physical habitat and prey abundance on habitat quality (Hayes et al. 2012; Rosenfeld et al. 2014). Incorporating discharge effects on drift abundance represents an additional layer of biological realism, and better understanding the significance of flow variation to drift production should become a priority for instream model development. Consistent with the prescription of Anderson et al. (2006), more advanced models are emerging that include some level of feedback between consumption and local resource abundance (e.g., Hayes et al. 2007, 2016) or use individual-based modeling to scale flow projections to population-level dynamics (Railsback et al. 2009; Ayllon et al. 2016). While promising, these models remain to be fully parameterized and validated before they can be applied in regular flow assessments. By maintaining the simplicity of the HSC as a biological model within existing instream flow modeling platforms, bioenergetic-based habitat suitability curves offer one potential avenue for bridging the transition to more realistic and dynamic modeling.

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Appendix: Habitat Suitability Values for Depth and Velocity

TABLE A.1. Velocity habitat suitability values for 6-, 8-, 10-, and 12-cm-FL juvenile Coho Salmon based on bioenergetics.

	Suitability			
Velocity (m/s)	6 cm FL	8 cm FL	10 cm FL	12 cm FL
0.00	0.00	0.00	0.00	0.00
0.02	0.27	0.21	0.18	0.16
0.04	0.51	0.41	0.35	0.31
0.06	0.71	0.60	0.51	0.46
0.08	0.86	0.75	0.66	0.60
0.10	0.95	0.88	0.78	0.73
0.12	1.00	0.96	0.88	0.84
0.14	0.97	1.00	0.95	0.91
0.16	0.92	0.98	0.99	0.97
0.18	0.80	0.94	0.99	1.00
0.20	0.62	0.87	1.00	0.99
0.25	0.00	0.52	0.77	0.88
0.30	0.00	0.00	0.29	0.58
0.40	0.00	0.00	0.00	0.00
0.50	0.00	0.00	0.00	0.00
0.60	0.00	0.00	0.00	0.00
0.70	0.00	0.00	0.00	0.00
1.20	0.00	0.00	0.00	0.00

TABLE A.2. Depth habitat suitability values for 6-, 8-, 10-, and 12-cm-FL juvenile Coho Salmon based on bioenergetics.

	Suitability			
Depth (m)	6 cm FL	8 cm FL	10 cm FL	12 cm FL
0.00	0.00	0.00	0.00	0.00
0.05	0.04	0.03	0.01	0.01
0.10	0.12	0.11	0.07	0.05
0.15	0.20	0.21	0.14	0.11
0.20	0.29	0.30	0.21	0.18
0.25	0.37	0.39	0.28	0.25
0.30	0.45	0.44	0.35	0.32
0.40	0.58	0.55	0.49	0.46
0.50	0.70	0.66	0.62	0.59
0.60	0.77	0.75	0.75	0.75
0.70	0.83	0.81	0.81	0.78
0.80	0.90	0.87	0.88	0.89
0.90	0.97	0.94	0.93	0.95
1.00	0.99	0.99	0.99	0.99
2.00	1.00	1.00	1.00	1.00