

Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat

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Abstract: The River Continuum Concept lacks a quantitative physical model to represent downstream trends in habitat. We evaluate whether hydraulic geometry relationships can be used as a physical template to predict longitudinal trends in habitat availability and optimal flows for different life-history stages of rainbow trout (*Oncorhynchus mykiss*). Optimal flows based on hydraulic geometry indicate that (i) optimal flows are higher for larger fish, (ii) optimal flows proportionally increase as streams became smaller and decrease downstream, and (iii) maximum predicted habitat suitabilities for fry and juveniles are in small streams, and maximum suitabilities are displaced progressively downstream for later life-history stages. These patterns are an emergent property of downstream increases in channel depth and velocity and changes in habitat suitability curves associated with increased swimming performance of larger fish. Nonlinear downstream trends in habitat imply that fixed flow percentages recommended by the Tenant method may substantially underestimate optimal flows in small streams. Despite oversimplifying complex channel structure, hydraulic geometry relationships should serve as a useful physical model for testing downstream trends in habitat-related processes along the river continuum.

Résumé : Il manque au concept du continuum fluvial un modèle physique quantitatif qui puisse représenter les changements de l'habitat vers l'aval. Nous vérifions si les relations de la géométrie hydraulique peuvent servir de cadre pour prédire les tendances longitudinales dans la disponibilité de l'habitat et les écoulements optimaux pour les différents stades du cycle biologique de la truite arc-en-ciel (*Oncorhynchus mykiss*). La géométrie hydraulique indique que (i) les écoulements optimaux sont plus élevés pour les poissons de plus grande taille, (ii) les écoulements optimaux augmentent de façon inversement proportionnelle à la taille du cours d'eau et ils diminuent vers l'aval et (iii) la majorité des habitats optimaux prédits pour les alevins et les jeunes truites se trouvent dans les cours de plus petite taille; ces optimums se déplacent progressivement vers l'aval pour les stades plus avancés du cycle biologique. Ces patrons sont des caractéristiques qui résultent des augmentations vers l'aval de la profondeur du chenal et de la vitesse du courant, ainsi que des changements dans les courbes de qualité de l'habitat associées à l'augmentation de la performance de nage des poissons plus grands. Les tendances non linéaires vers l'aval dans l'habitat ont comme conséquence que les pourcentages fixes de débit recommandés dans la méthode de Tenant peuvent sous-estimer considérablement les débits optimaux dans les petits cours d'eau. Même si elles simplifient trop la structure complexe des chenaux, les relations tirées de la géométrie hydraulique devraient pouvoir servir de modèle physique utile pour tester les tendances vers l'aval dans les processus reliés à l'habitat le long du continuum d'un cours d'eau.

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Introduction

Aquatic ecologists have long recognized that stream habitats change in predictable ways as they flow downstream, leading to longitudinal changes in biological communities and processes (e.g., Lotrich 1973; Naiman et al. 1987). The River Continuum Concept (Vannote et al. 1980) formalized the hypothesis that systematic habitat changes along a downstream gradient have predictable consequences for biological processes ranging from energy flow to community structure.

Despite a general appreciation of the pervasive influence of physical habitat on biological processes in streams (e.g., Statzner et al. 1988; Rabeni and Jacobson 1993) and the dominance of the River Continuum Concept as the central paradigm in fluvial ecology, there has been surprisingly limited development and use of physical models to quantify downstream trends in habitat.

Systematic downstream changes in habitat are of particular interest to fish ecologists because they affect both the nature and quantity of habitat available for fish, and therefore

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longitudinal trends in fish abundance and community structure (Schlosser 1982; Lamouroux 2007). In particular, downstream changes in channel size and water velocity will alter the quantity of habitat suitable for different species (or life-history stages) based on factors like swimming performance that affect ability to exploit different habitats. Available habitat is therefore sensitive to (i) channel dimensions and velocity as affected by location on the river continuum and (ii) the amount of water in the channel at any given time (discharge), which increases systematically downstream and also varies according to the natural flow regime (Poff et al. 1997) and anthropogenic demands (Poff et al. 2003).

Downstream changes in channel structure will therefore influence changes in habitat availability in unperturbed systems, as well as differential effects of water abstraction on available habitat along the river continuum, an increasing concern as human demand for water increasingly conflicts with the needs of natural ecosystems (Postel et al. 1996; Vörösmarty et al. 2000). Fish biologists typically assess habitat availability in streams using the instream flow incremental methodology (IFIM) in conjunction with some form of physical habitat simulation model (e.g., PHABSIM) that describes how the distribution of depth, velocity, and substrate in a stream changes at different flows. A habitat suitability model for the species of interest is then superimposed on simulations to evaluate which flows are optimal (i.e., generate the maximum amount of useable habitat). To understand how fish habitat and optimal flows for rainbow trout (*Oncorhynchus mykiss*), steelhead (anadromous *Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), and brown trout (*Salmo trutta*) vary as a function of stream characteristics, Hatfield and Bruce (2000) performed a meta-analysis on 127 PHABSIM studies from streams and rivers in western North America ranging in discharge from 0.1 to 400 m³·s⁻¹, representing the core of the native distribution of all three taxa. The most compelling pattern from their analysis was that optimal flows to maximize useable habitat varied systematically with stream size and location on the river continuum, confirming earlier observations from less comprehensive studies (e.g., Smith and Sale 1993; Jowett 1997). More specifically, optimal flows (as a percentage of mean annual discharge (MAD)) were found to generally increase as streams become smaller and decrease downstream, a pattern that was consistent for all four salmonid taxa. If there is a biological basis to this pattern, it has far-reaching implications for the management of stream flows, since the most common approach for determining instream flows in small streams (e.g., Tennant method; Tharme 2003) uses a fixed proportion of MAD irrespective of stream size.

As suggested by earlier studies (e.g., Jowett 1997), we hypothesize that downstream trends in habitat availability and optimal flows are the predictable outcome of interactions between downstream changes in average channel depth and velocity and the swimming performance characteristics of fish that influence habitat suitability. If this is the case, then the general patterns in both habitat availability and optimal flows observed by Hatfield and Bruce (2000) should be predictable using a physical habitat model that adequately represents the longitudinal habitat template in streams (e.g.,

downstream changes in depth and velocity; see Lamouroux and Capra (2002) for a similar analysis of the Hatfield and Bruce (2000) data set for brown trout).

In this paper, we explore the use of simple longitudinal hydraulic geometry relationships as a physical model to represent downstream trends in stream habitat. These relationships predict average channel width, depth, and velocity as power functions of stream discharge (eqs. 1, 2, and 3 below) and are a cornerstone of fluvial geomorphology (Leopold et al. 1964). Recent studies have demonstrated that average reach characteristics can be well-represented using simple hydraulic geometry relationships (e.g., Jowett 1998; Lamouroux and Jowett 2005). However, the suitability of simple hydraulic geometry relationships for representing longitudinal trends in fish habitat must be tempered by the observation that they implicitly ignore habitat complexity at smaller scales, effectively treating stream channels as uniform half-pipes, a gross oversimplification of channel complexity. Average estimates of channel depth and velocity from hydraulic geometry relationships fail to characterize (i) the small-scale heterogeneity associated with different substrate types and flows that create a patch mosaic in streams (e.g., Pringle et al. 1988), (ii) the transverse heterogeneity associated with shallow, slow water at stream margins and deep, fast water at the stream thalweg (Stewardson and McMahon 2002; Schweizer et al. 2007), (iii) or small-scale longitudinal variation in bed elevation associated with different habitat types (e.g., deep pools and shallow riffles). This small-scale complexity is pivotal to ecological processes in streams, and it is by no means certain that characterizing channels in terms of average characteristics — a single estimate of depth, velocity, and width at a section — can generate useful predictions of fish habitat and how it changes downstream.

Below, we describe the application of hydraulic geometry relationships to evaluating changes in fish habitat along the river continuum. We use both longitudinal (downstream) and at-a-station hydraulic geometry as a physical template to develop expectations for optimal flows and longitudinal trends in habitat availability for different life-history stages of rainbow trout (fry, juveniles, adults, and spawners) and compare our model predictions to empirical observations of optimal flows for rainbow trout from western North America (Hatfield and Bruce 2000). Our objectives are (i) to determine whether hydraulic geometry relationships can reproduce the empirically observed downstream trends in optimal flows for salmonids observed by Hatfield and Bruce (2000) (i.e., proportionally higher optimal flows in small streams; higher optimal flows for larger fish; and maximum habitat suitabilities for fry and juveniles in small streams); (ii) to provide a mechanistic basis for understanding why optimal flows may vary as a function of stream size; (iii) to determine how fish size or life-history stage affects expected longitudinal trends in available habitat; and finally, (iv) to evaluate the potential of hydraulic geometry relationships as a general physical template for predicting how biological processes change along the river continuum. We chose rainbow trout as the representative species for this analysis because it is widely distributed in streams and rivers, its biology (including habitat suitability curves) is well documented, and it showed qualitatively simi-

lar downstream trends in optimal flows to the other salmonids (steelhead, Chinook salmon, and brown trout) studied by Hatfield and Bruce (2000).

Overview of longitudinal and at-a-station hydraulic geometry

Longitudinal hydraulic geometry

Leopold and Maddock (1953) were the first to formally describe downstream trends in average channel width, depth, and velocity as simple power functions of river discharge:

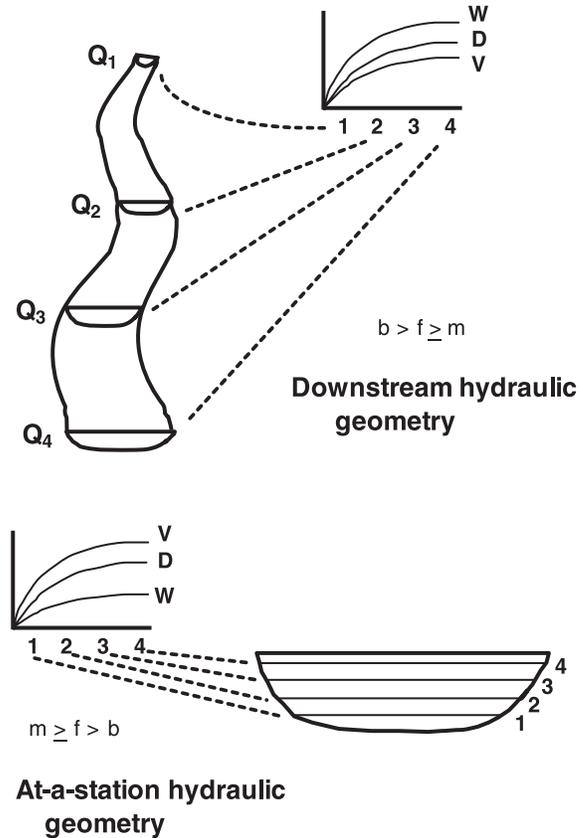
- (1) $w = aQ^b$
- (2) $d = cQ^f$
- (3) $v = kQ^m$

where w is average channel width; d is depth; v is velocity; Q is discharge; b , f , and m are exponents for the downstream rates of increase in width, depth, and velocity, respectively, with discharge; and a , c , and k are coefficients for the respective power functions. The assumption of continuity of discharge requires that the sum of the exponents equals 1 (i.e., an increase in depth requires a decrease in either width or velocity to maintain the same discharge), and similarly the product of the coefficients also has to equal unity ($b + f + m = 1$; $ack = 1$). These longitudinal relationships are empirically determined for a river basin by measuring channel width, depth, and velocity at multiple sites along a downstream gradient of increasing stream size at stable river flow (typically either bankfull stage or MAD, equivalent to average daily discharge; Fig. 1). The power function exponent is the slope of the log–log relationship, and the coefficient is the intercept; the coefficient can also be understood as the value of width, depth, or velocity when discharge is equal to $1 \text{ m}^3 \cdot \text{s}^{-1}$.

Because the exponents of the power functions are less than 1, the rates of increase of width, depth, and velocity decline as streams increase in size (Fig. 2). Differences in the rates of change of the three variables results in changes in average channel shape (e.g., width:depth ratio) along a downstream continuum. Because width invariably increases more quickly downstream than depth (modal values of $b = 0.4\text{--}0.5$; $f = 0.3\text{--}0.4$; $m = 0.1\text{--}0.2$; Park 1977), stream channels generally become relatively wider and shallower downstream, even though absolute width and depth increase with discharge. In essence, hydraulic geometry exponents describe the allometry of channel shape as streams increase in discharge.

The values of exponents range widely depending on the characteristics of a drainage basin (Park 1977; Richards 1977; Ferguson 1986), and differences in exponents represent an appealing way to characterize different types of streams with a minimum number of parameters, since exponent values change in predictable ways depending on basin gradient, substrate size, and riparian vegetation, among other factors (Hey and Thorne 1986; Millar 2005; but see Ridenour (2001) for a less optimistic view on consistent relationships between longitudinal hydraulic geometry and basin characteristics). Watershed gradient would appear to be the single most important factor influencing other exponents, with

Fig. 1. Downstream and at-a-station hydraulic geometry relationships. 1–4 represent either increasing discharge along a downstream continuum (upper panel) or increasing discharge at a single site (lower panel). The symbols b , f , and m represent the exponents for downstream rate of increase in width (W), depth (D), and velocity (V), respectively.

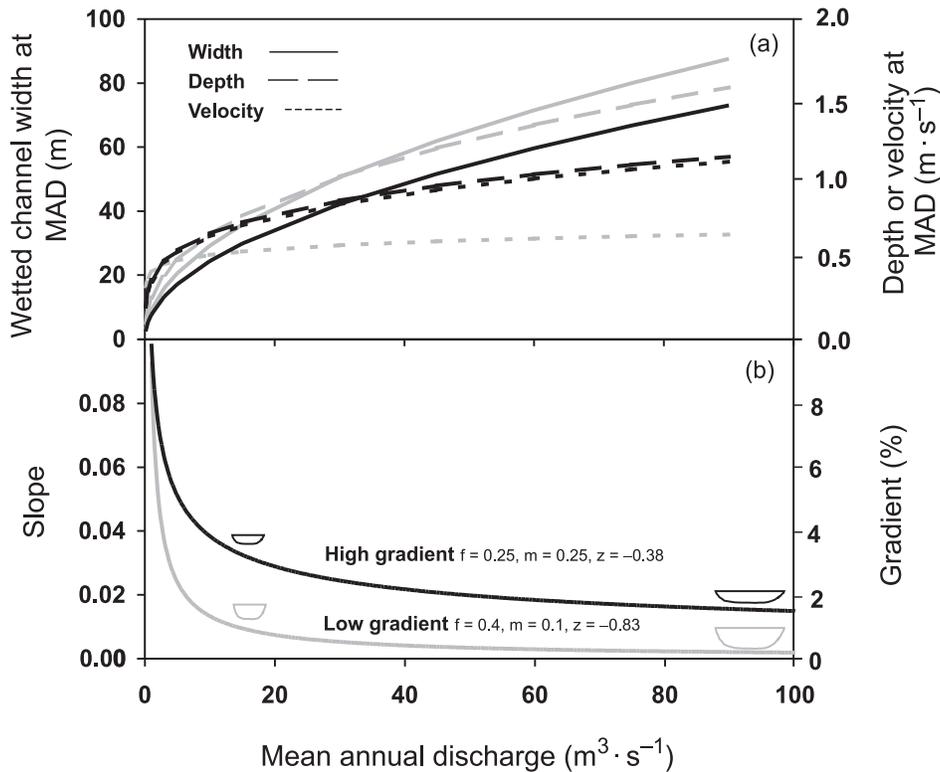


downstream velocity increasing more quickly (higher velocity exponent m) and depth more slowly (lower f) in steep basins (Fig. 2; Leopold et al. 1964), presumably as a consequence of greater roughness associated with larger substrate in steeper watersheds. The relationship between local slope and discharge can also be expressed as a power function, where

$$(4) \quad s = jQ^z$$

Unlike the exponents for other hydraulic geometry relationships, z is negative (i.e., local slope decreases with increasing stream discharge), and z is correlated with overall basin gradient. From this perspective, basin relief (steepness) can be viewed as an imposed constraint (Ferguson 1986) to which other factors (channel width, depth, and velocity) must adjust, although it should be recognized that fluvial geomorphologists also view local stream gradient as a response variable that adjusts to changes in sediment load and channel dimensions (Schumm and Lichty 1965). Average substrate size (roughness) appears to be the next most important factor influencing exponent values; an increase in average substrate size increases z (river gradient declines more slowly), thereby increasing downstream velocities (higher m ; Leopold et al. 1964).

Fig. 2. (a) Downstream hydraulic geometry relationships for high-gradient (black lines) or low-gradient (grey lines) drainage basins. (b) Changes in slope along a downstream gradient of increasing discharge assuming an exponent for downstream rate of decrease in channel roughness of -0.2 . MAD, mean annual discharge.



At-a-station hydraulic geometry

At-a-station hydraulic geometry describes the rate of change of channel width, depth, and velocity at a single site over a range of increasing discharge (Fig. 1) rather than at multiple sites at a single stage along the length of a river. The same power functions can be used to model at-a-station hydraulic geometry, but exponent values differ from downstream relationships. In contrast with downstream hydraulic geometry, width generally increases more slowly than either depth or velocity with increasing flow at a station (e.g., during a flood; Table 1). At-a-station hydraulic geometry parameters also vary with basin gradient (or watershed area; Dodov and Foufoula-Georgiou 2004), such that at-a-station velocity increases more quickly than depth in high-gradient basins (Table 1). Greater channel roughness associated with increased substrate size or bedform complexity also decreases the rate of change of velocity (m) and increases the rate of change in depth (f ; Leopold et al. 1964; Hey and Thorne 1986; Knighton 1998). At-a-station hydraulic geometry has also been applied to describe changes in fish habitat with varying discharge at a single station (e.g., Hogan and Church 1989; Jowett 1998).

Materials and methods

Hydraulic modeling scenarios

To develop a physical habitat template for the river continuum, we used longitudinal hydraulic geometry relationships (eqs. 1–3; Fig. 1; Table 1) to describe how average channel width, depth, and velocity change with increasing discharge

along a downstream continuum. (Discharge is viewed as a surrogate of distance from headwaters, since discharge is proportional to drainage area and therefore channel length (Knighton 1998). The absolute increase in channel length per unit discharge will depend on precipitation per unit area (i.e., streams in wet regions will generate greater discharge per unit area and therefore will have shorter channels for a given discharge).) Because basin gradient appears to be the single most important factor influencing longitudinal trends in channel morphology, we chose two contrasting sets of hydraulic geometry exponents representing high- and low-gradient basins to test how basin gradient affects downstream trends in fish habitat. Since velocity in high-gradient basins increases more quickly downstream (Fig. 2) to approach velocities that may exceed the tolerances of all life-history stages of fish (Fig. 3), we would predict that lower-gradient streams should have greater habitat availability at a given discharge, and therefore higher optimal flows for maximizing fish habitat. Note that a key assumption of our comparison of high and low gradient scenarios is a consistent relationship between longitudinal hydraulic geometry exponents and basin characteristics. Although supported by theory (Leopold et al. 1964), empirical support for this assumption is more ambiguous (e.g., Ridenour 2001; Wohl 2004).

For the high-gradient scenario, we used downstream and at-a-station hydraulic geometry exponents from a set of 73 New Zealand river reaches presented by Jowett (1998), with mean discharges ranging from 0.6 to $204 \text{ m}^3 \cdot \text{s}^{-1}$. Both downstream and at-a-station velocity coefficients for these

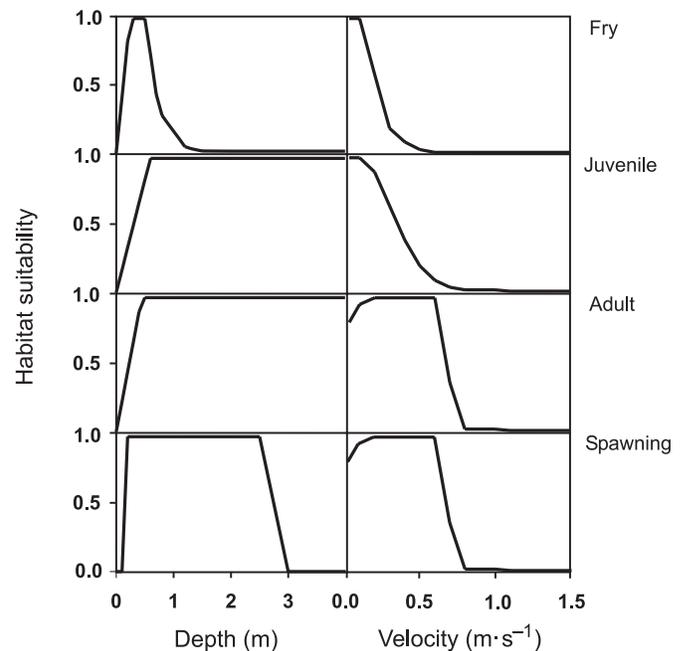
Table 1. Hydraulic geometry exponents and coefficients used in modeling scenarios.

Parameter	Downstream hydraulic geometry				At-a-station hydraulic geometry			
	Exponent		Coefficient		Exponent			
					Average		Riffle	
High gradient								
Width	<i>b</i>	0.5	<i>a</i>	7.8	<i>b</i>	0.21	—	—
Depth	<i>f</i>	0.25	<i>c</i>	0.37	<i>f</i>	0.34	<i>f</i>	0.44
Velocity	<i>m</i>	0.25	<i>k</i>	0.36	<i>m</i>	0.45	<i>m</i>	0.33
Low gradient								
Width	<i>b</i>	0.5	<i>a</i>	9.23	<i>b</i>	0.26	—	—
Depth	<i>f</i>	0.4	<i>c</i>	0.26	<i>f</i>	0.4	<i>f</i>	0.52
Velocity	<i>m</i>	0.1	<i>k</i>	0.42	<i>m</i>	0.34	<i>m</i>	0.22

streams tend to be higher (Table 1) than the averages presented by earlier reviews (Leopold and Maddock 1953; Park 1977), presumably reflecting the relatively steeper relief of New Zealand drainages (e.g., Biggs et al. 1990; Molnar and Ramirez 2002). For the low-gradient scenario, we used downstream and at-a-station exponents from the classic study of Leopold and Maddock (1953). Half of the rivers in the Leopold and Maddock (1953) data set came from low-relief topography in the central US plains (Kansas, South Dakota, and Nebraska), and the rest were from low- to intermediate-gradient rivers of the high western plateau (Wyoming, New Mexico, and Utah). Because the salmonid streams analyzed by Hatfield and Bruce (2000) came from the relatively steep topography of western North America (British Columbia, Alaska, Washington, Oregon, and California), we used the New Zealand (high gradient) exponents as the downstream model for comparing hydraulic geometry habitat predictions with empirical observations of optimal flows. (We implicitly assume that the higher longitudinal velocity exponent for New Zealand streams relative to the Leopold and Maddock data set is due to higher basin relief in New Zealand rather than differences in channel roughness exponent). We estimated z (the downstream rate of change of slope) in the low- and high-gradient scenarios as -0.38 and -0.83 , respectively, using relationships derived from fig. 7–27 in Leopold et al. (1964; based on the Manning equation (Richards 1982), with $z = -3.16f + 1.4y + 0.65$, where y is the exponent for the relationship between channel roughness and discharge, and the width exponent is constant at $b = 0.5$). Assuming an average downstream rate of change of roughness of -0.2 (Leopold 1994) and substituting the equation for z above into eq. 4, f is related to local slope s as $f = [(\{[\log(s) - \log(j)]/\log(Q)\} - 1.4y - 0.65)/3.16]$. We estimated downstream change in slope assuming $j = 0.1$ (slope of 0.1 at $Q = 1 \text{ m}^3 \cdot \text{s}^{-1}$).

To test the prediction that basin gradient affects longitudinal trends in habitat availability and optimal flows, we compared predictions of optimal flows between high- and low-gradient scenarios. Our simulations (and downstream hydraulic geometry relationships in general) are somewhat unrealistic in that they assume continuous longitudinal trends in channel metrics and river gradient. Real rivers exhibit downstream discontinuities in slope and sediment inputs (Ward and Stanford 1983; Poole 2002; Wohl 2004). These could be treated as local discontinuities in down-

Fig. 3. Depth and velocity habitat suitability curves for different life-history stages of rainbow trout (*Oncorhynchus mykiss*).



stream exponents, but for simplicity we only consider continuous scenarios.

We used the separate high- and low-gradient downstream hydraulic geometry relationships to estimate average channel width, depth, and velocity at MAD for 12 downstream stations (0.1, 0.5, 1, 3, 10, 15, 30, 45, 60, 75, and 90 $\text{m}^3 \cdot \text{s}^{-1}$) along a longitudinal gradient of increasing river discharge. At each of these 12 stations, we then used the corresponding high- or low-gradient at-a-station hydraulic geometry relationships to model how average channel width, depth, and velocity changed with increasing discharge at each station. Hydraulic geometry coefficients at each station were fit based on at-a-station exponents for low- or high-gradient scenarios (Table 1) and the estimates of wetted width, depth, or velocity imposed by downstream hydraulic geometry. Fitted hydraulic geometry coefficients showed relationships with stream discharge similar to those observed elsewhere (e.g., Stewardson 2005). To provide a more intuitive metric of stream size for comparative purposes, we also estimated

channel bankfull width as a function of discharge, assuming that MAD was on average 13% of bankfull discharge (Leopold 1994). (This assumption will tend to overestimate channel bankfull width when MAD is a higher proportion of bankfull discharge.)

Estimation of optimal flows along a downstream gradient

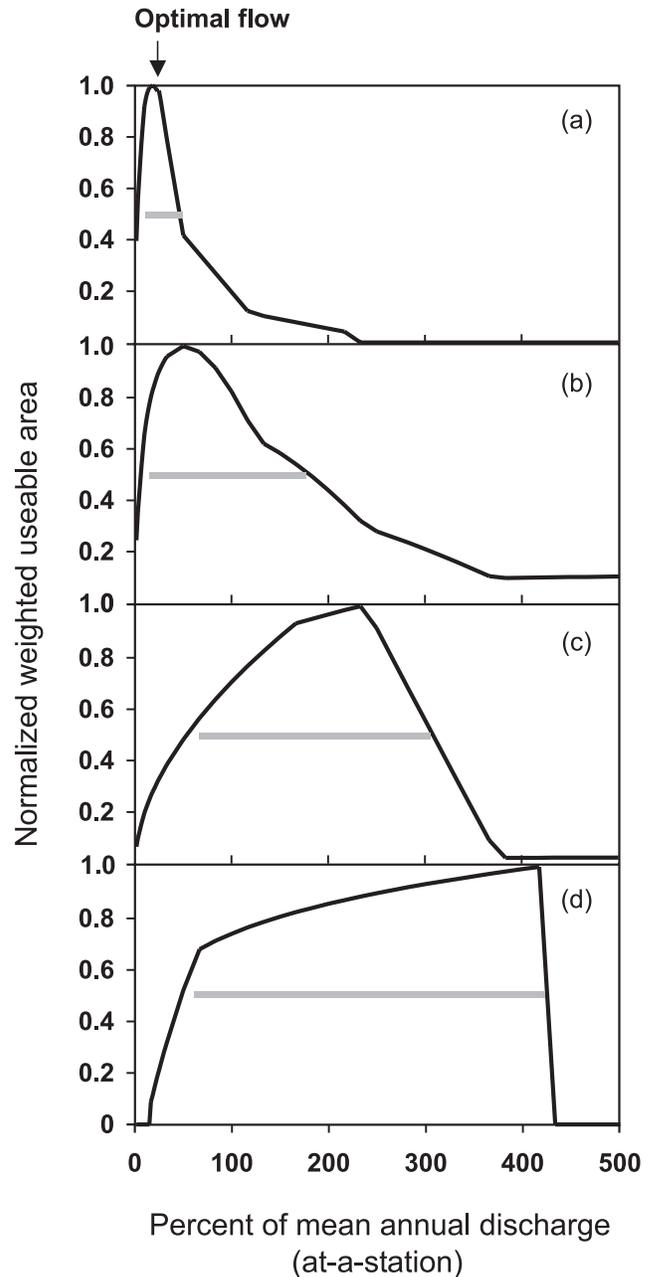
We used rainbow trout habitat suitability curves (Raleigh et al. 1984; Fig. 3) to calculate habitat suitability and weighted useable area over a range of flows at each downstream station for each life-history stage of rainbow trout (fry, juveniles, adult, and spawning; Fig. 4). Habitat suitability curves are generally based on frequency of use of different microhabitats in the wild and are standardized to a maximum of 1 (Bovee 1982; Mathur et al. 1985). Estimates of optimal flow using IFIM and PHABSIM typically use habitat suitability curves for depth, velocity, and substrate; we used suitability curves for velocity and depth only, since hydraulic geometry models do not predict substrate size. IFIM generates estimates of weighted useable area (WUA, a composite of habitat quality and habitat area) by multiplying the habitat suitability values associated with modeled depth, velocity, and substrate in each PHABSIM habitat cell to derive a composite habitat suitability score, which is then multiplied by cell area to generate WUA per cell; cell values of WUA are then summed for a site (Bovee 1982; Parasiewicz and Dunbar 2001).

We converted mean velocity and depth estimated using hydraulic geometry to modal velocities and depths by multiplying by 0.87 and 0.79, respectively (after Jowett 1998), to generate modal estimates that more accurately represent available habitat for skewed distributions. To estimate WUA with our simplified hydraulic geometry data, we calculated WUA at multiple discharges at each station based on the product of the habitat suitability values for average channel depth and velocity multiplied by channel wetted width. Optimal flow was determined as the flow that maximized WUA for each life-history stage (Fig. 4). Habitat suitability curves and the WUA approach have a variety of shortcomings that compromise their ability to accurately represent true habitat quality (e.g., Mathur et al. 1985; Rosenfeld 2003; Rosenfeld et al. 2005); however, the estimates of useable habitat and optimal flows summarized by Hatfield and Bruce (2000) are based on IFIM and WUA, constraining us to use the same approach for comparative purposes. While estimates of WUA may provide poor estimates of habitat quality, they may provide a more reasonable representation of the amount of habitat that falls within the performance limits of a particular life-history stage (Rosenfeld et al. 2005).

Refinement of optimal flow predictions using pool-riffle hydraulic geometry

Because hydraulic geometry relationships estimate average channel characteristics and ignore variance in velocity and depth, they may provide poor estimates of habitat availability for organisms using habitats with higher or lower velocities than the channel average. For example, if spawning fish use high-velocity riffle habitat (Fig. 3), average channel velocities will underestimate the velocity of their preferred habitat at a given discharge and therefore overestimate opti-

Fig. 4. Weighted useable area vs. discharge at a single station (mean annual discharge (MAD) = $3 \text{ m}^3 \cdot \text{s}^{-1}$) for rainbow trout (*Oncorhynchus mykiss*) fry (a), juveniles (b), adults (c), and spawners (d). Weighted useable area is divided by the maximum at a site to standardize to a value of 1. Grey lines represent the range of discharge over which the weighted useable area exceeds 50% of the maximum.



mal flows. To test whether incorporating heterogeneity in velocities and depths associated with pool and riffle structure could improve predictions of optimal spawning flows, we also estimated optimal spawning flows using different at-a-station hydraulic geometry parameters for pool and riffle habitats.

The effect of pool and riffle habitat on at-a-station rates of change in velocity and depth is well documented (Richards 1977; Knighton 1998) and has been described as velocity re-

versal or flow convergence (Wilkinson et al. 2004). At bankfull stage, differences in bed elevation associated with pools and riffles exert less influence on total water depth, so that velocities and depths tend to converge across habitats. At low discharge, pools are deeper and slower than riffles, but as stream flow increases with a rising hydrograph velocity in pools increases more quickly than velocity in riffles (Fig. 5), leading to velocity reversal if pool velocity exceeds riffle velocity. In effect, pools may switch from being depositional habitats at low flows to erosional ones at high flows, with the opposite being true for riffles. Associated differences in the hydraulic geometry exponents for pools and riffles have been observed (Richards 1977; Knighton 1998). We modeled velocities and depths in riffle habitats by symmetrically increasing the depth exponent and decreasing the velocity exponent by 0.12 (Fig. 5; Table 1), a value that approximates the differences in exponents between pools and riffles observed in a number of studies (e.g., Richards 1977; Knighton 1998; Halket and Snelgrove 2005).

To derive coefficients for riffle hydraulic geometry equations, we estimated riffle depth by first modeling residual pool depth (RD_{pool}) as a function of bankfull channel width (W_{bf} ; $R^2 = 0.67$, $F_{[1,5]} = 10.4$, $P < 0.024$) using data from rivers in California (Madej 1999; using the 75th percentile of pool depths from 1995 when channels were least aggraded):

$$(5) \quad RD_{\text{pool}} = 0.057(W_{\text{bf}})^{0.534}$$

Total pool depth at a given discharge was estimated as the sum of average depth (predicted by hydraulic geometry) and residual pool depth, and average pool velocities were estimated based on continuity of discharge. Increased velocity in riffles was assumed symmetrical with decreased velocity in pools, and riffle depth was estimated assuming continuity of discharge. We assumed equivalent widths in pools and riffles.

Downstream trends in habitat suitability

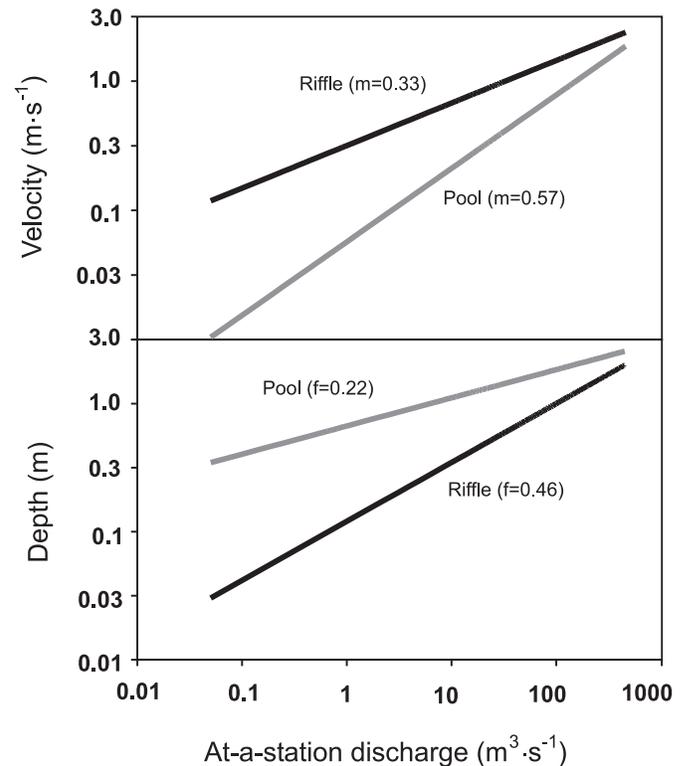
Longitudinal trends in fish abundance and habitat suitability represent the interaction of performance tolerances of different life-history stages (Fig. 3) and downstream increases in velocity and depth. For instance, if smaller fish have lower maximum sustained swimming speeds, then habitat suitability for fry and juveniles should decline as velocities increase downstream. To evaluate how habitat suitability for different life-history stages is expected to change along a downstream continuum, we modeled habitat suitability and WUA for fry, juveniles, adults, and spawners at all 12 downstream stations at MAD.

Results

Observed vs. modeled longitudinal trends in optimal flows

Hatfield and Bruce (2000) fit power functions to empirical estimates of optimal flows for different life-history stages (Fig. 6a), which clearly show that optimal flows (as a percentage of MAD) are (i) higher in smaller streams and (ii) progressively higher for larger life-history stages. Predicted optimal flow curves based on hydraulic geometry re-

Fig. 5. Contrasting rates of change of velocity and depth with increasing discharge in pools and riffles (for mean annual discharge (MAD) = $3 \text{ m}^3 \cdot \text{s}^{-1}$).

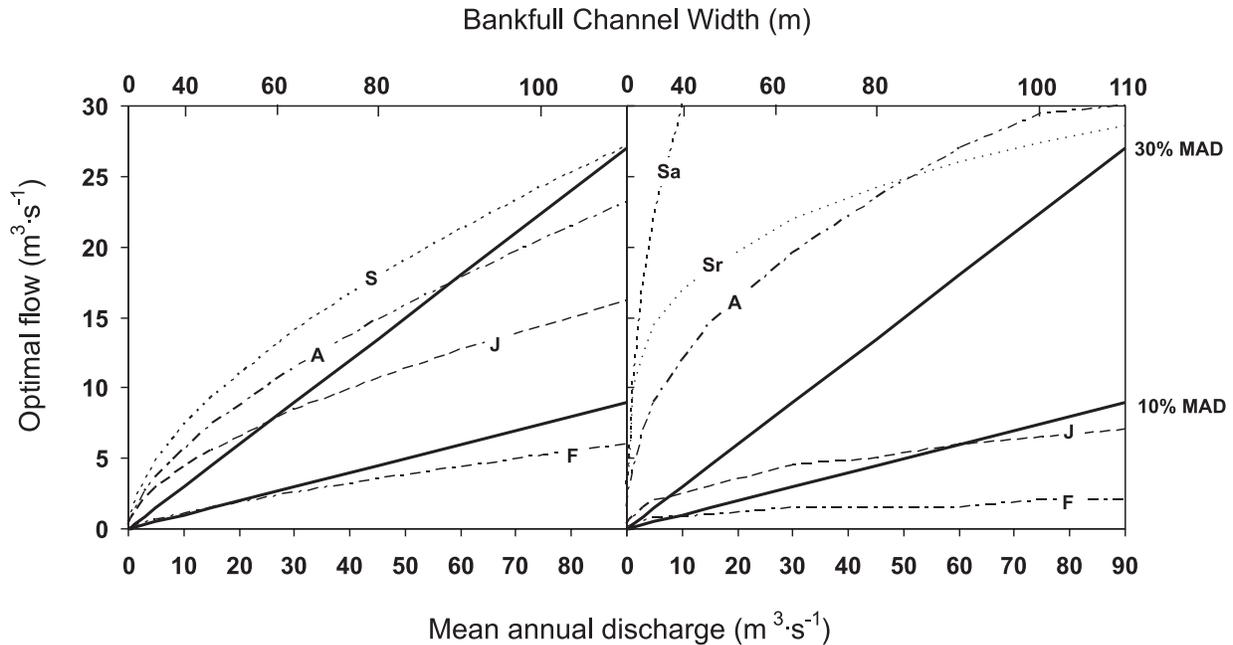


produced both of these attributes (Fig. 6b). Optimal flows for individual life-history stages predicted by hydraulic geometry (Fig. 6b) showed the same general shape as the empirical relationships from Hatfield and Bruce (2000), with predicted optimal flow as a proportion of MAD higher in small streams. Hydraulic model predictions also ranked optimal flows for different life-history stages in the same order, with highest optimal flows predicted for spawning habitat, followed by adult, juvenile, and fry habitat. The actual precision with which hydraulic geometry predicted the best-fit line to average optimal flows observed by Hatfield and Bruce (2000) was far less accurate and generally outside of the 95% confidence intervals of the empirical relationships (Fig. 7). Optimal flows for fry and juveniles were generally underestimated using hydraulic geometry (Fig. 6b), and optimal flows for adults and spawners were systematically overestimated.

The overestimate in predicted optimal flows was most pronounced for spawning habitat (S_a , Fig. 6b; Fig. 7). Optimal flows estimated using habitat suitability and WUA in riffle habitat (i.e., using riffle hydraulic geometry exponents rather than channel average exponents) dramatically improved the shape and accuracy of the optimal flow curve for spawning (S_r , Fig. 6b). This supports the expectation that incorporating variance in velocity and depth associated with smaller-scale habitat structure (i.e., including the distribution of velocity and depths rather than average values) greatly improves predictions of habitat availability and optimal flows.

The implicit assumption of the Tennant approach that optimal flows are independent of stream size was not substanti-

Fig. 6. Observed (a) and modeled (b) optimal flows for different life stages of rainbow trout (*Oncorhynchus mykiss*) plotted against mean annual discharge (MAD) along a downstream gradient. Modeled habitat availability and optimal flows use hydraulic geometry exponents for steeper drainages from Jowett (1998). F, fry; J, juveniles; A, adults; S, spawning; S_a and S_r represent spawning habitat modeled using average or riffle depth and velocities, respectively. Straight lines represent Tennant (1976) flow criteria of 10% and 30% of MAD.



ated by either the empirical or hydraulic model relationships. Deviation of predicted optimal flows from Tennant recommendations (i.e., straight lines representing 10% and 30% MAD in Fig. 6) is greatest for very small and very large streams. The Tennant instream flow recommendations (10% MAD as a minimum short-term flow for aquatic organism survival, 30% MAD as good conditions, and 60% MAD as optimal; Tennant 1976) fit reasonably well with the empirically observed optimal flows for fry in small streams with $MAD < 1 \text{ m}^3 \cdot \text{s}^{-1}$ (Fig. 7), although they fall below the optimal flows for fry predicted by hydraulic geometry. However, optimal flows for juveniles predicted by both empirical and hydraulic geometry relationships greatly exceed the fixed Tennant recommendations in small streams (Fig. 7). Hydraulic geometry modeling also indicates that fry and juvenile habitat is most sensitive to deviation from optimum (narrow peaks in WUA; e.g., Fig. 4), likely as a consequence of the narrower depth and velocity tolerances of early life-history stages (Fig. 3).

Longitudinal trends in habitat in high- vs. low-gradient basins

As expected, optimal flows for the low-gradient scenario exceeded those of the high-gradient scenario for most life-history stages (Fig. 8). Higher optimal flows also imply greater available habitat at optimal flow in lower-gradient streams; for example, estimates of WUA were on average 1.5 times higher for fry and 4 times higher for juveniles in the low-gradient scenario. This modeling indicates that optimal flows are sensitive to basin gradient as well as stream size, causing fixed-flow Tennant recommendations to further underestimate optimal flows in low-gradient streams. Closer

fit of modeled to empirical optimal flows using the New Zealand high-gradient hydraulic geometry exponents supports the assumption that they are more representative of the relatively steep topography of the data set analyzed by Hatfield and Bruce (2000) than exponents from the lower gradient rivers sampled by Leopold and Maddock (1953).

Downstream trends in habitat suitability by life-history stage

Longitudinal trends in habitat suitability and WUA at mean annual discharge in the high-gradient scenario indicate that habitat suitability for fry peaks in the smallest streams ($< 5 \text{ m}$ bankfull channel width; Fig. 9) at MAD, habitat suitability for juveniles peaks at $\sim 10 \text{ m}$ bankfull channel width, and habitat for adults and spawners peaks at channel widths on the order of 40 m . WUA generally peaks further downstream than habitat suitability, indicating that declining habitat suitability downstream may be partially offset by increasing area of useable habitat as channels become wider. As discharge decreases, optimal habitat for all life stages tends to be displaced downstream (Fig. 9).

Predictions of habitat suitability and WUA for adults goes to zero downstream, highlighting the limitations of using average channel depth and velocity to calculate habitat suitability and WUA. When the average downstream channel velocity exceeds the threshold suitability limits of adult fish (Fig. 3), predicted WUA based on channel averages goes to zero; using a frequency distribution of depths and velocities (i.e., incorporating variance in velocity and depth associated with slower pools and channel margins; Lamouroux et al. 1995; Stewardson and McMahon 2002) would remedy this anomaly and more realistically predict the presence of suit-

able habitat at higher average channel velocities. It is also worth noting that we have greater confidence in our estimates of optimal flows than WUAs, since the location of the peak in optimal flow (Fig. 4) will be insensitive to consistent biases in WUA estimates.

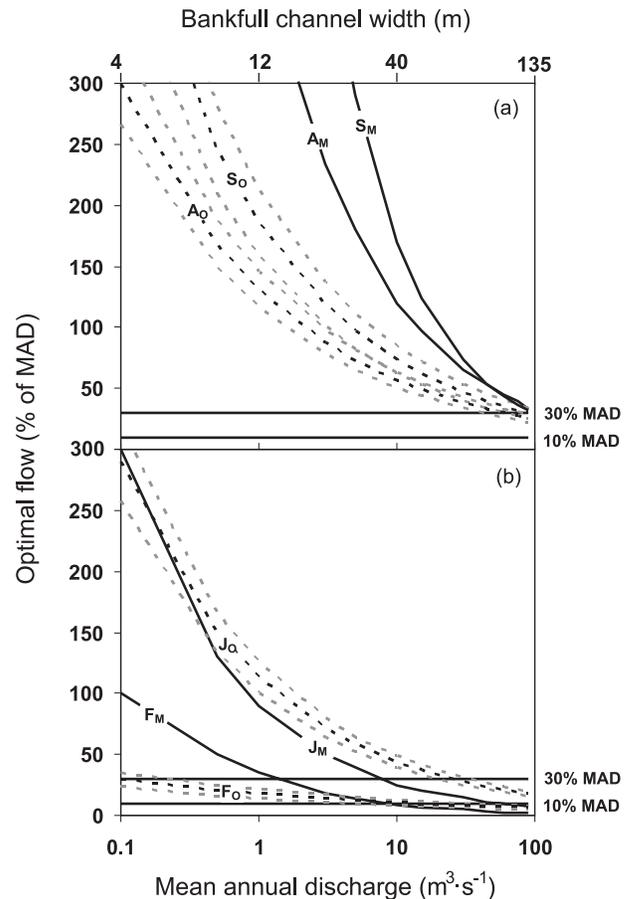
Discussion

Despite their simplicity, basic hydraulic geometry relationships reproduced the general longitudinal trends in optimal flows observed for salmonid streams in western North America. Hydraulic geometry relationships demonstrated that (i) optimal flows are higher for larger fish (later life-history stages), (ii) optimal flows (as a percentage of MAD) generally increase as streams became smaller and decrease downstream, and (iii) maximum predicted habitat suitability for fry and juveniles are in small streams, and maximum suitabilities are displaced progressively downstream for later life-history stages and lower flows. These are the same conclusions drawn by Hatfield and Bruce's (2000) empirical analyses of 127 PHABSIM studies for stream salmonids from western North America. These conclusions are also supported by an earlier reanalysis of the Hatfield and Bruce (2002) data set by Lamouroux and Capra (2002), who also demonstrated that optimal flows for adult brown trout could be predicted from simple reach characteristics (width, depth, discharge, and bed grain size).

The observed longitudinal trends in habitat and optimal flow are an emergent and predictable outcome of size-related performance tolerances of fish (as represented by habitat suitability curves) and downstream hydrology (increases in depth and velocity) along the river continuum. For example, the generally lower velocity and depth preferences of smaller fish tend to constrain their optimal habitat to smaller streams. While the shape, order, and magnitude of optimal flow relationships from hydraulic geometry were similar to observed relationships, model predictions were usually outside of empirical confidence intervals. In the form presented here, hydraulic geometry relationships should be viewed as a habitat template (process) model that captures general downstream trends and patterns rather than as a predictive model for estimating optimal flows for individual streams. Moving towards empirical models of longitudinal trends in habitat availability and optimal flows based on hydraulic geometry will require further empirical studies relating hydraulic geometry parameters to basin characteristics.

Nevertheless, the concordance of optimal flow predictions with empirical relationships is remarkable, given the simplifying assumptions involved. For instance, the published hydraulic geometry parameters that we applied to high-gradient streams came from a landscape (New Zealand) with similar relief to the reference data set (western North America), but we have no way of knowing how accurately they represent the true reference stream parameters. Similarly, the individual studies summarized by Hatfield and Bruce (2000) estimated optimal flows using a variety of different habitat suitability curves for rainbow trout, often based on observations of habitat use in individual streams. Many of these instream flow studies also used habitat suit-

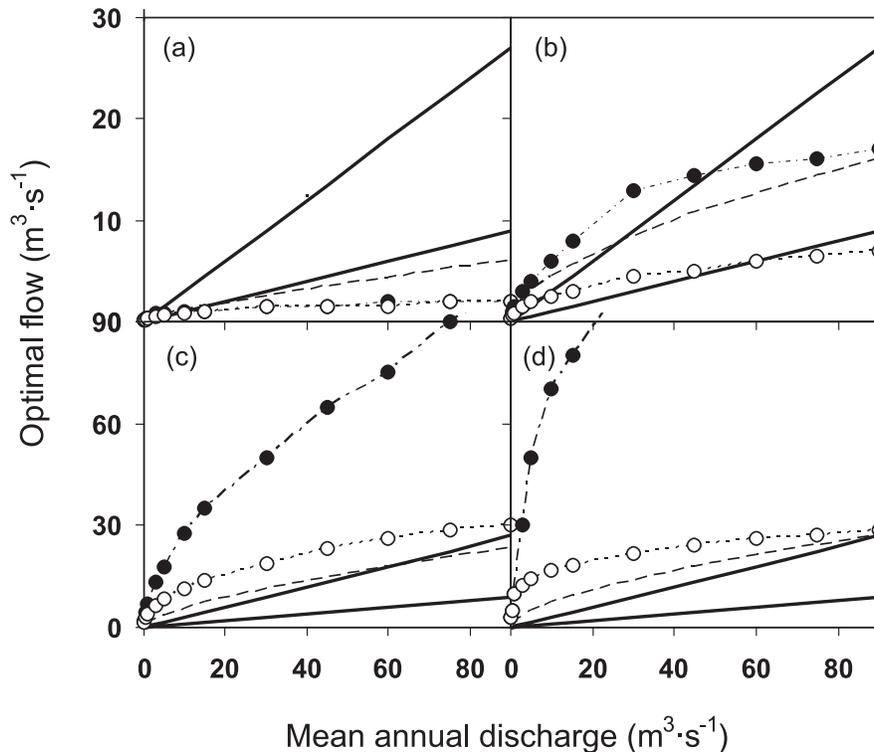
Fig. 7. Observed and modeled optimal flows as a percentage of mean annual discharge (MAD) for (a) adult (A) and spawning (S) rainbow trout (*Oncorhynchus mykiss*) and (b) fry (F) and juveniles (J). Broken lines are observed optimal flows (F_O, J_O, A_O, S_O) from Hatfield and Bruce (2000), and solid lines are modeled optimal flows (F_M, J_M, A_M, S_M) using high-gradient hydraulic geometry exponents from Jowett (1998). Horizontal lines represent 10% and 30% of MAD. Broken grey lines represent 95% confidence intervals for estimates of observed optimal flow from Hatfield and Bruce (2000).



ability curves for substrate in their estimation of WUA, while our simplified estimates were based solely on velocity and depth. Given these multiple sources of error, the fit of the hydraulic geometry predictions is surprisingly good and indicates that the general form of the underlying relationships (and therefore the inferences that can be made from them) is extremely robust. This is supported by the observation that Hatfield and Bruce (2000) observed qualitatively similar relationships for both steelhead and Chinook salmon.

The main shortcoming of downstream hydraulic geometry for estimating fish habitat is that estimates of average channel velocity and depth, even when extremely accurate, lead to biases in habitat availability because the variance (i.e., the proportion of habitat above and below the mean) is undescribed (Singh and Broeren 1989; Moody and Troutman 2002). For example, at flows where mean velocities exceed the tolerance of fry ($0.5 \text{ m}\cdot\text{s}^{-1}$), predicted fry habitat based

Fig. 8. Predicted optimal flows for high-gradient (open circles) and low-gradient streams (solid circles) by life-history stage: (a) fry, (b) juvenile, (c) adult, (d) spawners. The broken line without symbols represents observed optimal flows from Hatfield and Bruce (2000). Solid lines represent Tennant (1976) flow recommendations of 10% (lower line) and 30% (upper line) mean annual discharge (MAD).



on channel means will be zero, even though fry habitat may be present in shallow water at stream margins (Rao et al. 1993). The predictive value of accounting for small-scale heterogeneity in channel structure is demonstrated by the improved fit of optimal spawning flows when riffle hydraulic geometry exponents are used. This approach, however, still provides only a mean estimate of channel depth and velocity in riffle habitat. A frequency distribution of depths and velocities at a site, rather than a simple mean, should provide much more accurate estimates of useable habitat and optimal flows (Rao et al. 1993). Distributions can be generated directly from empirical measurements or from probabilistic models that predict the frequency distribution of depth and velocity around average values (e.g., Lamouroux et al. 1995; Stewardson and McMahon 2002; Schweizer et al. 2007). Recent models that predict the joint probability distribution of depth and velocity (e.g., Schweizer et al. 2007) may prove to be a more robust approach to account for longitudinal variation in velocity and depth than the use of different hydraulic geometry exponents for pools and riffles, as presented here.

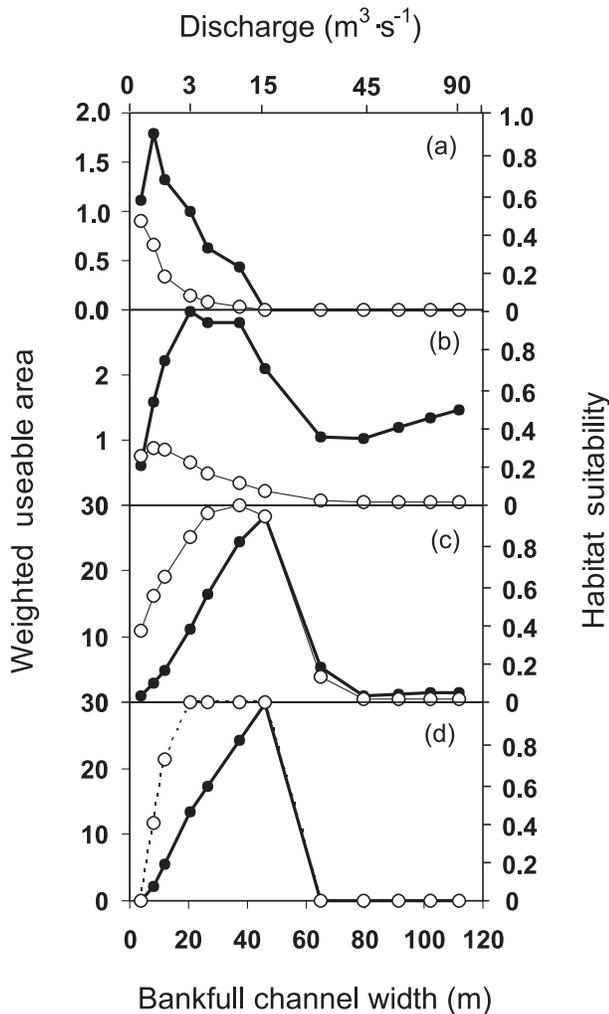
The most directly applied result of our analysis is that optimal flows must vary as a function of stream size, as previously noted by Hatfield and Bruce (2000) and earlier authors (e.g., Annear and Conder 1984; Smith and Sale 1993; O'Shea 1995; Lamouroux and Capra 2002). The application of fixed-proportion-of-flow criteria (e.g., Tennant approach) irrespective of channel size may therefore seriously under- or over-estimate optimal flows depending on stream size. This is most pronounced for small streams and

larger rivers, where the deviation from Tennant recommendations is greatest. Underestimation of optimal flows is of greatest concern for smaller streams, which are rarely allocated the resources for a formal flow assessment and therefore default to fixed-proportion-of-flow management. While the empirically estimated optimal flows for fry fall within the recommended Tennant flow range for channel widths <12 m, both empirical and modeled optimal flows for juveniles greatly exceed even the Tennant recommendation of excellent flows (60% MAD) at channel widths <20 m ($3 \text{ m}^3 \cdot \text{s}^{-1}$ MAD). If the fish population of interest is limited by abundance of juveniles rather than fry (often the case for many salmonids, e.g., anadromous cutthroat trout (*Oncorhynchus clarkii*) or steelhead), then the Tennant flow recommendation may be inappropriate and have the potential to substantially impact a population. If the population is limited by adult habitat (e.g., resident fish), then even higher flows may be required.

Overestimation of optimal flows in larger rivers using the Tennant approach is probably less of a management concern than underestimation of flows in small streams. Modeled and observed optimal flows for adults are above or close to 30% MAD even for the larger stream size in our analysis ($90 \text{ m}^3 \cdot \text{s}^{-1}$ MAD). Although lower flows are predicted to be optimal for fry and juveniles in larger streams, if juvenile life stages are not limiting the population because of abundant rearing habitat in smaller tributaries, then downstream flows should be managed to maximize habitat for adults (i.e., higher rather than lower flows).

This also highlights two potentially competing objectives of flow regulation: maximizing the amount of habitat for a

Fig. 9. Weighted useable area (solid circles) and average habitat suitability (open circles) vs. channel width or longitudinal discharge for fry (a), juvenile (b), adult (c), or spawning (d) rainbow trout (*Oncorhynchus mykiss*) at mean annual discharge.



target species or life-history stage vs. maintaining a natural flow regime that maximizes biological integrity of the natural system (Orth 1987; Jowett 1997; Poff et al. 1997). Managing flows for a single juvenile life stage requires maintaining higher flows in smaller streams and relatively lower flows in larger ones, leading to convergence of hydraulic conditions on an optimum defined by the habitat suitability curves of a taxon that tends to reduce the natural contrast in stream character along the river continuum (Jowett 1997). If the management goal throughout a river profile is to maximize abundance of juvenile salmonids with lower velocity requirements, then differentially reducing flows in larger downstream reaches may facilitate this goal. However, if the goal is to maintain suitable biological conditions for the suite of life-history stages, species, and processes that normally occur in longitudinal succession along the river continuum, then managing for low flows that create optimal habitat for a single juvenile life stage may be inappropriate (Tharme 2003; Anderson et al. 2006). Restoration of lower-velocity side-channel habitat along river main stems may be a more appropriate way to increase juvenile habitat

without adversely affecting other species or biological processes that are dependent on higher flows. In contrast, managing for higher base flows in smaller streams may be appropriate when juvenile salmonids are the most abundant taxa present in a low-diversity system, as is often the case.

Our analysis also needs to be tempered by the understanding that the logic behind WUA as an index of habitat availability is flawed for a number of reasons (Mathur et al. 1985; Garshelis 2000). For instance, a large area of marginal habitat (e.g., velocity and depth suitability <0.25) can generate the same WUA value as a small area of highly suitable habitat, even though the marginal habitat may not permit substantial growth or survival. Even if WUA gives an accurate representation of available habitat, changes in flow simultaneously affect habitat for multiple life-history stages as well as the production of their prey, making it difficult to infer population-level effects based on changes in WUA alone. The WUA-IFIM approach cannot predict a population response without some understanding of the effect of habitat on abundance, population limitation, and recruitment of individuals between life stages (Kocik and Ferreri 1998; Gouraud et al. 2001; Railsback et al. 2003), that is, populations may be limited by habitat for fry, juveniles, or adults (Capra et al. 2003; Anderson et al. 2006; Rosenfeld and Hatfield 2006). To truly understand the population-level effects of changes in flows, flow models that predict changes in habitat need to be linked to stage-structured population models (e.g., Sabaton et al. 1997; Bartholow et al. 2001; Gouraud et al. 2001) within a landscape context (Fausch et al. 2002). Ideally, these models should also account for flow effects on processes other than fish habitat, such as effects of flow on production of invertebrate prey, maintaining temperature or water quality in a nonlethal range, or maintenance of channel structure, to name a few (White 1976; Jowett 1997; Anderson et al. 2006).

Our hydraulic geometry analysis also ignores transverse structure associated with the floodplain (e.g., side-channel habitat) and habitat that may become available at flood discharges (i.e., floodplain habitat); in tropical rivers, juvenile rearing habitat may be most abundant at extremely high flows rather than extremely low flows (Junk et al. 1989). Similarly, side-channel and floodplain habitat that is wetted at low to moderate flows in temperate rivers is not captured by simple hydraulic geometry, but is especially important because it displaces juvenile rearing habitat much further downstream than it would normally be predicted to occur when a channel is modeled as a half-pipe.

A hydraulic geometry approach to characterizing physical habitat can be potentially useful in both a landscape and River Continuum context. In a landscape context (Fausch et al. 2002), hydraulic geometry can be used to characterize habitat patches within a drainage network, where the distribution of habitat patches suitable for different life-history stages and the ability of fish to move between them ultimately determine the size and viability of populations (Schlosser 1991, 1995; Kocik and Ferreri 1998). In a River Continuum context, our analysis of optimal flows indicates that hydraulic geometry can be successfully applied as a habitat template to test explicit hypotheses of longitudinal change in ecological processes along the river continuum. While hydraulic geometry relationships performed reason-

ably well for predicting optimal flows, the inclusion of small-scale habitat structure (e.g., longitudinal and transverse heterogeneity in channel depth and velocity; Stewardson and McMahon 2002) will generate much more realistic estimates of available habitat. Future model refinement should focus on (i) including depth and velocity distributions based on empirical data or probabilistic models (e.g., Schweizer et al. 2007) and (ii) estimating habitat availability at a drainage network scale by taking into account the abundance of streams of different sizes within a basin.

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