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THE INFLUENCE OF VARIABLE HABITAT SUITABILITY CRITERIA ON PHABSIM HABITAT INDEX RESULTS

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ABSTRACT

The Physical Habitat Simulation System (PHABSIM) still probably remains as the most widespread habitat method used to establish inflow standards or to link habitat temporal variations with fish population dynamics. However, statistical uncertainties around the PHABSIM main output, the weighted usable area (WUA) over discharge curves, are usually ignored. Here, we assess the uncertainty in WUA curves and derived habitat duration curves induced by the variability around the PHABSIM biological model, the habitat suitability criteria, using brown trout *Salmo trutta* as the model species. Bootstrap analyses showed that the uncertainty around the WUA curves was rather high when bootstrap sample (BS) size was low and differed among age classes, being generally lower for young-of-the-year (YOY). Width of 95% confidence intervals for maximum WUA magnitude increased with decreasing BS size, ranging from 19.3% for YOY trout at the largest BS size (40 transects, 270 habitat use observations) to 146% for juveniles at the smallest BS size (nine transects, 60 habitat use observations). The uncertainty arose primarily from the construction of the channel index variable. Nevertheless, results showed that the uncertainty in WUA values could be reduced down to acceptable levels by using general functional channel index categories. Likewise, the shape of WUA curves was also highly variable when BS was small. These patterns resulted in habitat duration curves being highly uncertain, much more in their amplitude than in their shape. Uncertainty about the flows corresponding to different habitat exceedance values increased with decreasing probability of exceedance. Width of peak flow confidence intervals ranged from 3.3% for YOY trout at the largest BS size to 226% for adults at the smallest BS size. Yet such levels of uncertainty do not necessarily entail critical errors in the decision-making process because large variability in flow peak does not necessarily lead to large variability in WUA magnitude. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: habitat suitability criteria; habitat simulation models; environmental flow assessment; uncertainty; bootstrap

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INTRODUCTION

It is now widely accepted that human water demands must be balanced with the needs of rivers, but tensions in water resource allocation are intensifying because of both growing human demand and uncertainties in the water needs of riverine ecosystems themselves under climate change context (Petts, 2009). This concept of ensuring adequate water for aquatic ecosystems is a key element in many international policies and in the water law of many countries. Under the European Water Framework Directive (2000/60/EEC) in particular, implementation of environmental flows is one of the measures needed to restore or to maintain 'good ecological status' and can be included in the River Basin Management Planning process (Acreman & Ferguson, 2010).

Tharme (2003) identified more than 200 different methodologies that have been described around the world to determine environmental flows, these methods being categorized into four main types. Within them, habitat simulation methodologies ranked second in frequency of applications at a global scale. The Instream Flow Incremental Methodology (Stalnaker *et al.*, 1995) and its popular associated software, the Physical Habitat Simulation System (PHABSIM), is one of the most widespread and advocated habitat methods. Habitat simulation models integrate a hydraulic model with a biological model of habitat selection, the habitat suitability criteria (HSC), to calculate the variation of a habitat index called weighted usable area (WUA) as a function of discharge.

Regardless of its widespread use, the hydraulic and biological aspects of PHABSIM have been also the subject of continuing criticism since its formal introduction (e.g. Marthur *et al.*, 1985; Shirvell, 1986; Castleberry *et al.*, 1996; Ghanem *et al.*, 1996; Kondolf *et al.*, 2000). One of the main concerns deals with the uncertainty associated to PHABSIM main output, the WUA–discharge curves. Williams (1996) found that the widths of the confidence intervals were substantial and that the shape of the composite WUA curve was highly uncertain. For these reasons, Castleberry *et al.* (1996) stated that estimates of WUA should be reported with standard errors or confidence

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intervals so that decision-makers are informed of the uncertainty associated with the estimates. In spite of these caveats, the statistical uncertainty in PHABSIM results has ever since been largely ignored, and only a few studies have addressed the issue (e.g. Payne *et al.*, 2004; Gard, 2005). The lack of reaction to uncertainty contrasts with many other ecological research areas which are becoming increasingly aware of the importance of accurately accounting for multiple sources of variability when modelling ecological phenomena and making forecasts (Lek, 2007). This fact recently led Williams (2010) to revisit the topic, showing that results of 1-D PHABSIM studies could be even more uncertain than previously reported.

Aside from simulation errors derived from the inability of 1-D hydraulic models to adequately predict velocity fields in complex natural streams (Kondolf *et al.*, 2000), which may be reduced in 2-D models (Gard, 2009; Waddle, 2010), uncertainty in PHABSIM results directly arises from measurement and sampling issues. Sources of variability include location and number of transects (Williams, 1996, 2010; Kondolf *et al.*, 2000; Payne *et al.*, 2004; Gard, 2005), errors in measurement of habitat variables within transects (Williams, 1996, 2010; Kondolf *et al.*, 2000) and procedures used for HSC development. However, little consideration has been given to the uncertainty arising from the biological models in PHABSIM despite the fact that consistency of results from habitat simulation models relies heavily on the accuracy of the HSC (Heggenes *et al.*, 1996). Indeed, the reliability of the HSC may have the strongest influence on output quality (Petts, 2009). The main objectives of this study were as follows: (i) to estimate the uncertainty in WUA–discharge relationships and derived habitat duration curves resulting from the variability of HSC; and (ii) to determine which habitat variables primarily drive such uncertainty. Brown trout *Salmo trutta* was used as the model species.

STUDY AREA

The studied river was located in northern Spain and corresponded to the Mediterranean headwater mountain stream reach type described in Ayllón *et al.* (2010a), i.e. low stream order (2), short distance from the origin (7 km), small watershed size (18 km^2), high reach gradient (5%), narrow width (5 m), very low slow to fast water ratio (<0.1), and hence low mean reach depth (12 cm), maximum reach depth below 45 cm and medium depth to width ratio (40) during summer conditions.

MATERIALS AND METHODS

Data collection

The study was carried out during the summer of 2004. Electrofishing using a 2200-W DC generator rather than snorkel survey were used to collect habitat use data because some areas within the reach were either too shallow or too turbid to be snorkelled. Captured trout were measured (fork length, to the nearest millimetre) and weighed (to the nearest gramme). Scales were taken for age determination so that each individual could be assigned to one of three age classes, young-of-the-year (YOY; 0+), juvenile (1+) or adult (>1+). The fish were placed into holding boxes to recover and then returned back to the stream. Numbered tags were dropped wherever a trout was captured, and depth, current velocity, substrate and cover were measured afterwards in a 1-m^2 quadrat. Depth and current velocity were measured once at the exact point where the trout was captured, while the proportion of substrate and cover were visually estimated within the surface of the quadrat. A total of 105 YOY, 114 juvenile and 80 adult trout were captured.

Physical habitat availability data were collected concurrently with fish sampling. Habitat availability was estimated every 1 m along 44 transects placed perpendicular to the flow. Physical habitat variables were measured in 4.75 ± 1.30 verticals per transect on average. The transects were systematically set 5 m apart, and sampling was stratified by habitat type. Total depth (cm), current velocity (m s^{-1}), substrate composition and cover were measured. The proportion (%) of substrate and cover were visually estimated in a 1-m^2 quadrat. Substrate was classified according to modified categories from classification by Platts *et al.* (1983) as silt (particle size less than 0.8 mm), sand (0.8–4.7 mm), gravel (4.8–76.0 mm), cobble (76.1–304.0 mm), boulder (more than 304.0 mm) and bedrock. We defined cover as any element other than substrate that can provide protection to fish against predators or adverse environmental conditions. The type of cover was classified as vegetation (aquatic or overhanging), woody debris, undercut bank, combined cover (combination of vegetation and woody debris), pools and under cascade.

Habitat suitability criteria

Univariate habitat suitability curves for water depth, current velocity and channel index were developed by age classes. The channel index is a categorical variable used in habitat simulation models to describe the structural characteristics of the stream channel (see Bovee, 1986). In the present study, the channel index was established as a combination of substrate and cover features. Whenever an element providing cover was present, it was considered the main structural element of the quadrat, whereas dominant substrate represented channel index when no cover elements were available in the quadrat. Based on this criterion, two different channel index curves were calculated. Channel index 1 was classified in 12 categories according to the substrate and cover classes previously defined. Channel

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index 2 was classified in seven categories because some of the defined substrate and cover classes were merged into functional groups. Hence, cobble and boulder categories were grouped and considered as substrate velocity shelters. Silt and sand were treated as a common category (fines). All cover categories were grouped because they refer to elements which mostly provide visual shelter against predators in locations near banks.

Initially, channel index suitability curves were built through use-to-availability ratios: histograms of frequencies of use and availability were elaborated for each channel index category, and the corresponding suitability index was calculated as the ratio between proportional use and availability and then normalized, dividing by the maximum suitability value. Subsequently, univariate resource selection functions (RSFs) were developed to calculate depth and velocity suitability curves. RSFs described the relationship between water depth and current velocity availability and the relative probability of habitat use. An RSF is then a probabilistic form of habitat suitability criteria (Ahmadi-Nedushan *et al.*, 2006). RSFs were preferred over the use-to-availability ratio method because they are statistically and quantitatively more rigorous (Boyce *et al.*, 2002). Functions were developed by means of logistic regressions, following the procedures described by Hosmer & Lemeshow (2000). Linear and polynomial functions were fitted to data, competing models being compared by means of the Akaike's Information Criterion adjusted for small samples for final model selection (Burnham & Anderson, 2002). Significance level was set at $\alpha = 0.1$. Finally, RSFs were normalized so that the minimum value was 0 and the maximum was 1.

Uncertainty in flow–habitat relationships and habitat duration curves as a function of HSC variability

A bootstrap analysis (Efron & Tibshirani, 1993) was used to estimate the uncertainty in WUA curves resulting from HSC development. Systematic samples were treated as if they were random samples. Therefore, as Williams (1996, 2010) pointed out, results from this study apply to a model stream reach type rather than to the specific studied reach. In each replicate, bootstrap samples (BS) of transect data and fish observations were selected and HSC calculated. Firstly, samples of 40, 33, 26, 22, 16 and nine transects (corresponding to 90, 75, 60, 50, 35 and 20% of the full set of transects) were drawn randomly without replacement from the full set of transects, with stratification by habitat type, to define habitat availability (Table I); similarly, an equally proportionate number of habitat use observations were also drawn randomly from the complete set. Microhabitat suitability curves were developed from habitat use and transect bootstrap sample data according to the aforementioned methodology. Finally, the HSC developed at each bootstrap replicate were used to calculate the WUA curves for the full set of transects. To do this, physical habitat simulations were carried out with the PHABSIM software. Hydraulic data were calibrated in PHABSIM following procedures in the study of Milhous *et al.* (1989). Hydraulic conditions were simulated for 25 discharges, from 0.02 to 3.5 m^3 s^{-1}. PHABSIM simulations were performed over the full set of transects, and not only over transects encompassed in the bootstrap sample, to isolate the effects of sample size on WUA curves due to HSC variability from the effects of transect number in the simulation process. This process was repeated for 200 replicates, a number that should be large enough to ensure that the results are stable (Gard, 2005). The percentile bootstrap was used to estimate the 95% confidence limits for WUA curves, which were computed as the interval containing the central 190 replicate WUA curves at each simulated discharge. The coefficient of variation of maximum WUA was calculated as well. In addition, normalized WUA curves and associated confidence intervals were calculated to estimate the uncertainty in the shape and position of WUA curves. Confidence intervals for normalized WUA at a given discharge were estimated in the same way as with WUA. Likewise, confidence intervals around developed HSC were also computed following the same procedure.

Table I. The number of transects in the full set and six bootstrap samples (90, 75, 60, 50, 35 and 20% of full set) used to develop HSC, by habitat type

Habitat type	Full set	BS 90%	BS 75%	BS 60%	BS 50%	BS 35%	BS 20%
Cascade	2	2	1	1	1	0	0
Rapid	9	8	7	5	5	4	2
Riffle	9	8	7	5	4	3	2
Run	22	20	17	14	11	8	4
Shallow pool	2	2	1	1	1	1	1
Deep pool	0	0	0	0	0	0	0
	44	40	33	26	22	16	9

Sensitivity analyses were carried out to determine which microhabitat variables accounted for most of the variance in WUA curves resulting from HSC development. To estimate uncertainty derived from one single microhabitat variable, each bootstrap replicate WUA curve was constructed using the suitability curve of the evaluated variable, developed from the replicate bootstrap sample, while fixing the other variables by using the specific age class suitability curves calculated with the full data set of transects and habitat use observations.

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In a second stage, uncertainty around derived habitat duration curves was assessed. Habitat duration curves represent the amount of time that a particular magnitude of WUA is equalled or exceeded on a habitat time series. In each replicate, WUA was processed through a time series analysis using the daily flow data provided by the nearest gauging station for the last 15 years. Daily flow values greater than 3.5 $m^3 s^{-1}$ were eliminated from the analysis (2% of total data). Habitat duration curves were constructed afterwards by sorting the habitat data from highest to lowest and by expressing each data point as a percentage of the total number of values. Normalized habitat duration curves were also built. In both cases, confidence intervals were estimated in the same way as with WUA–flow relationships.

Finally, the uncertainty in the flow value corresponding to the WUA value associated with the different exceedance percentiles was also estimated. Because the WUA curve is typically bell-shaped, some portion of the habitat duration curve represents levels of habitat produced under both high- and low-flow conditions. That is to say, habitat values associated with some exceedance percentiles may be due to both a high or low discharge in the period of record. In those cases, the lowest flow value was selected.

RESULTS

Results from PHABSIM simulations performed with the HSC based on the full set of transects (Figure 1) showed that the WUA curve for 0+ age class resulted in higher WUA values than older ones' at any simulated discharge. The peak flow for the WUA curves ranged from 0.37 to 0.65 $m^3 s^{-1}$ for 0+ and >1+ age classes, respectively. As expected, decreasing number of transects used to develop the HSC increased the width of the confidence intervals around the HSC (Figure 1) and hence the confidence limits of WUA curves (Figure 2). The coefficient of variation of maximum WUA increased with decreasing BS size from 5.2 to 25.7% in YOY, from 5.5 to 45.7% in juveniles and from 7.3 to 34.2% in adults. This meant that the 95% confidence limits on the mean (expressed as a percentage of the mean) increased from 19.3 to 93.8% in YOY, from 20.7 to 145.0% in juvenile and from 46.6 to 126.5% in

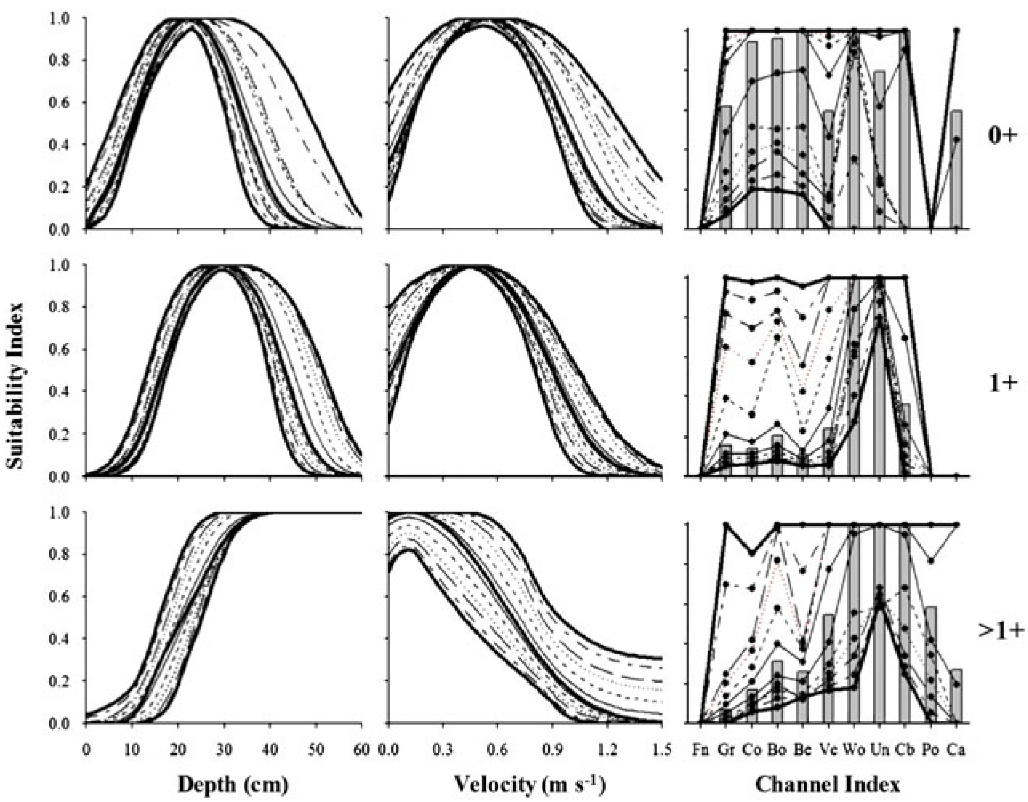

Figure 1. Habitat suitability criteria for 0+, 1+ and >1+ age classes based on the full set of 44 transects (inside thick solid line; grey bar) and their corresponding confidence intervals based on bootstrap samples of 90% (40 transects; inside thin solid line), 75% (33), 60% (26), 50% (22), 35% (16) and 20% (nine; outside thick solid line) of the full set of transects. Channel index categories refer to fines (Fn), gravel (Gr), cobble (Co), boulder (Bo), bedrock (Be), vegetation (Ve), woody debris (Wo), undercut bank (Un), combined cover (Cb), pool, (Po) and under cascade (Ca).

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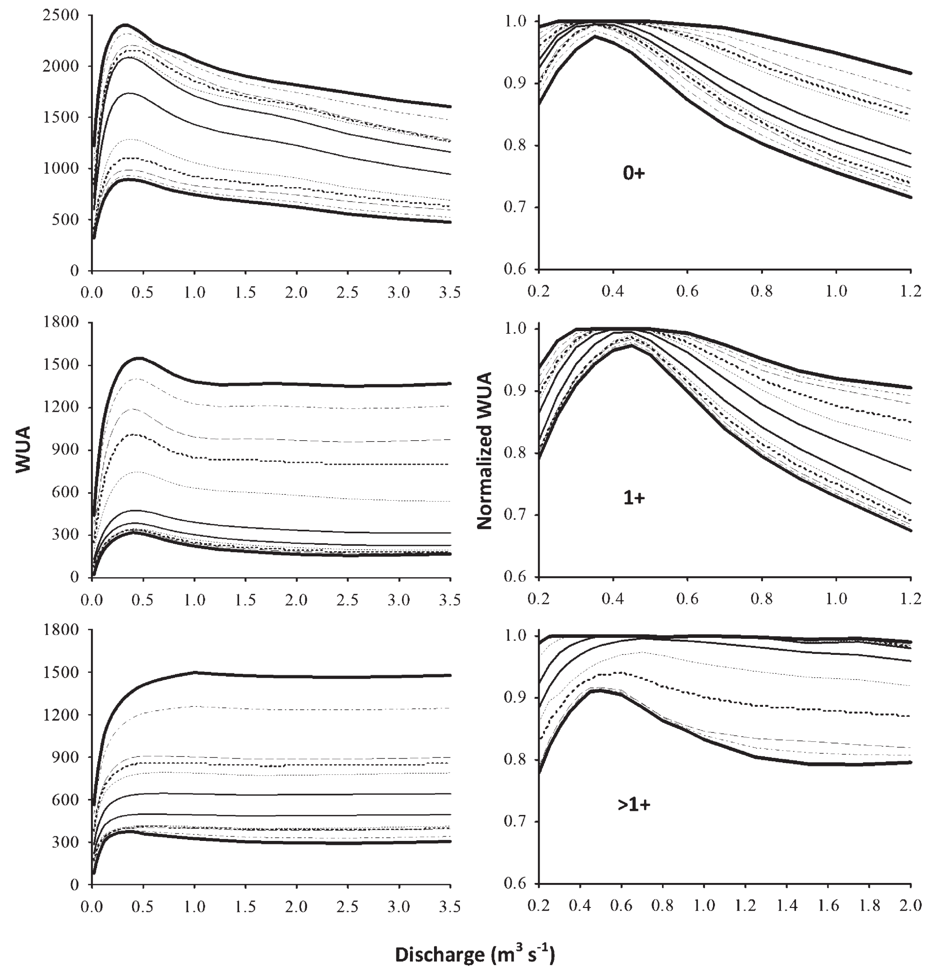

Figure 2. Bootstrap 95% confidence intervals for WUA and normalized WUA curves over simulated discharges based on bootstrap samples of 90% (40 transects; inside thin solid line), 75% (33), 60% (26), 50% (22), 35% (16) and 20% (nine; outside thick solid line) of the full set of 44 transects for 0+, 1+ and >1+ age classes. Normalized WUA graphs show the range of discharge near the peaks of WUA–discharge curves.

adult trout. Not only the magnitude but also the shape of WUA curves was subjected to a high uncertainty, as it was shown by the normalized WUA curves (Figure 2). The confidence interval for the peak flow ranged from 0.37–0.41 to 0.29–0.51 $m^3 s^{-1}$ (from 3.6 to 59.5% of the mean) for YOY WUA, from 0.42–0.47 to 0.37–0.57 $m^3 s^{-1}$ (from 11.6 to 46.5% of the mean) for juvenile WUA and from 0.55–1.10 to 0.32–1.81 $m^3 s^{-1}$ (from 84.6 to 226.0% of the mean) for adult WUA.

Sensitivity analyses showed that most of WUA magnitude uncertainty arises from channel index variability, irrespective of BS size or age class (Table II). In contrast, most of the uncertainty in flow peak was induced by water velocity variable, especially at smaller BS sizes. Uncertainty in maximum WUA for all age classes was significantly reduced at smaller BS sizes when channel index 2 was used to perform PHABSIM simulations (Table II). The coefficient of variation of maximum WUA was reduced down to 20.0, 20.2 and 21.9% for YOY, juvenile and adult trout, respectively, at the smallest BS size. However, the uncertainty in the peak flow was very similar either using channel index 1 or 2 in the simulations.

Derived habitat duration curves were also highly uncertain, much more in amplitude than in shape (Figure 3). At the smallest BS size, the 95% confidence limits on the mean WUA value associated to any given exceedance percentile were always higher than 93.4, 146.7 and 114.1% for YOY, juvenile and adult trout, respectively. These values were fairly constant across the different habitat exceedance percentiles. However, the uncertainty around the normalized habitat duration curves was significantly smaller. The width of confidence limits around the normalized WUA values increased with increasing exceedance percentile but were always lower than 28.5, 38.2 and 52.7% of the mean for YOYs, juveniles and adults, respectively, at the smallest BS size.

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Table II. Results of sensitivity analyses of the uncertainty in WUA–discharge relationships generated by the variability of each microhabitat variable at different bootstrap samples. Bootstrap 95% confidence interval on the mean (expressed as a percentage of the mean) for maximum WUA and flow associated with maximum WUA by age classes are shown

BS	Habitat variable	0+		1+		>1+	
		max WUA	Flow at max WUA	max WUA	Flow at max WUA	max WUA	Flow at max WUA
90%	Depth	3.7	1.3	2.2	9.9	3.2	6.7
	Velocity	3.2	3.3	3.5	11.1	6.5	51.8
	Channel index 1	25.1	2.3	29.5	10.7	23.2	13.3
	Channel index 2	30.6	2.8	25.1	10.1	28.6	11.8
75%	Depth	9.6	11.5	9.3	10.8	10.6	15.4
	Velocity	9.8	14.8	7.1	14.9	20.7	104.6
	Channel index 1	42.9	12.2	64.7	11.9	57.2	30.8
	Channel index 2	32.3	10.7	27.9	12.6	33.0	26.7
50%	Depth	14.0	24.0	10.7	31.0	14.0	36.4
	Velocity	13.9	27.3	11.7	64.5	25.4	104.6
	Channel index 1	72.3	16.5	118.7	15.9	85.2	50.9
	Channel index 2	48.8	13.5	37.2	16.9	46.1	70.2
20%	Depth	23.3	40.6	21.9	42.9	26.7	62.0
	Velocity	21.2	62.2	17.2	80.5	36.0	201.7
	Channel index 1	78.6	30.9	144.0	19.9	109.2	74.2
	Channel index 2	67.3	26.8	79.2	21.9	77.7	78.1

BS, bootstrap sample.

The uncertainty in the flow values that correspond to the WUA values associated with the different exceedance percentiles increased with both decreasing BS size and exceedance percentile (Figure 4). In fact, the highest uncertainty was linked to the maximum WUA, while it was non-existent above the 90th percentile at any BS size. Below the 50th exceedance percentile, the confidence limits on the mean associated flow were around 8% at the largest BS size and around 50% at the smallest BS size for YOYs, 10 and 35% for juveniles, and 10 and 70% for adults.

DISCUSSION

In the present study, bootstrap analyses showed that confidence intervals around the WUA curves were rather wide when the number of transects used to estimate habitat availability was low. The uncertainty arose primarily from the construction of the channel index variable. Likewise, the shape and position of WUA curves can be highly uncertain when BS is small, resulting mainly from variability around the water velocity suitability curves. The patterns observed in the WUA–flow relationships generated a high uncertainty in the magnitude and shape of derived habitat duration curves.

The uncertainties of habitat modelling results estimated here were substantial and of the same order of magnitude estimated previously for other fish (e.g. Gard, 2005; Williams, 2010), mammal (Bender *et al.*, 1996) or bird (Burgman *et al.*, 2001; Van der Lee *et al.*, 2006) species. This considerable level of uncertainty is suggested to be inherent to HSI models (e.g. Williams, 1996; Van der Lee *et al.*, 2006). Regarding PHABSIM studies, our results show that, at small BS size, the uncertainty in WUA magnitude at any given discharge resulting from HSC variability can be similar to that derived from sampling and measurement problems associated with accurately representing a river reach (Williams, 1996, 2010). Sensitivity analyses showed that uncertainty in WUA magnitude was mainly generated by channel index variability. In contrast, most of the uncertainty in the shape of WUA curves, and hence in peak flow, primarily resulted from the variability in water velocity suitability curves. This result was expected because PHABSIM does not simulate changes in structural elements with changes in flow. Therefore, the channel index SI commonly has a multiplier effect on the WUA results, influencing the magnitude of the WUA values, but not the overall shape of the WUA–discharge curve, which depends upon the hydraulic variables (Maddock *et al.*, 2004). However, in cases where the channel index is stratified with discharge (e.g. bands of riparian vegetation), it will affect the overall shape.

Because the width of confidence intervals around WUA curves was driven by variability in SI scores of channel index categories, a higher uncertainty is expected in age classes that preferentially use structural elements with low availability in the stream reach because they could be misrepresented in the BS, especially when the number of transects set to estimate habitat availability is low. That was

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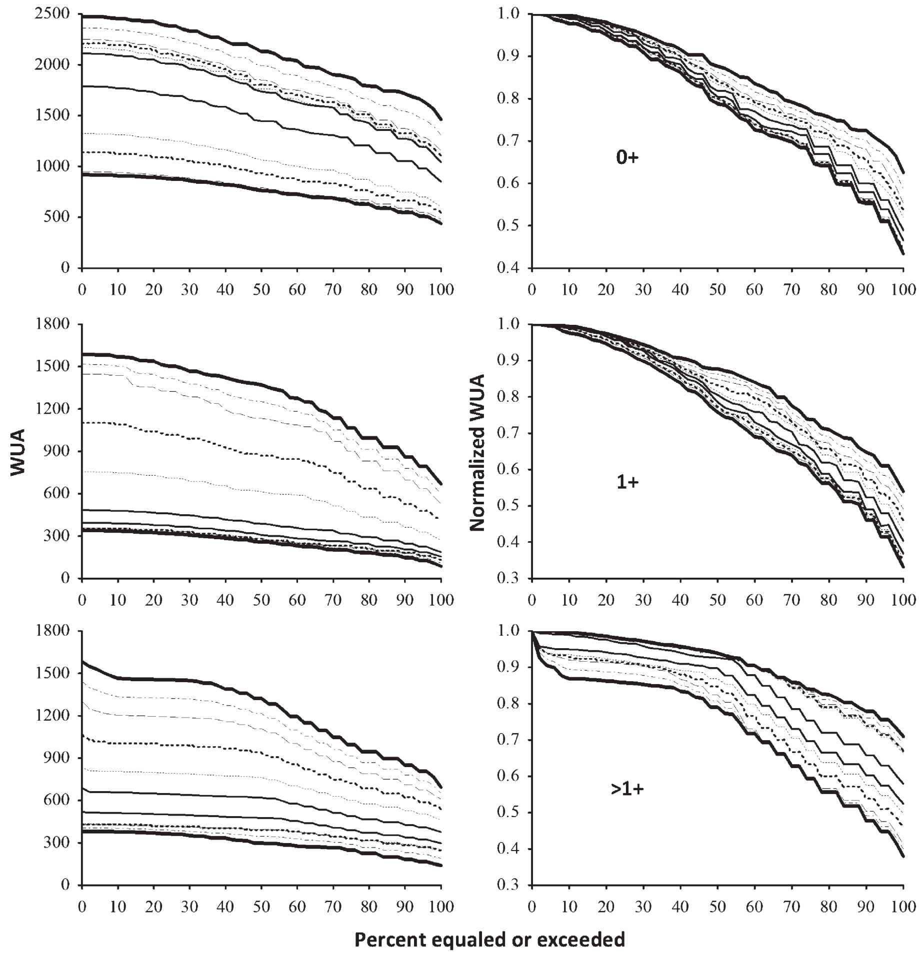

Figure 3. Bootstrap 95% confidence intervals for habitat duration and normalized habitat duration curves based on bootstrap samples of 90% (40 transects; inside thin solid line), 75% (33), 60% (26), 50% (22), 35% (16) and 20% (nine; outside thick solid line) of the full set of 44 transects for 0+, 1+ and >1+ age classes.

evidenced by the patterns of change in suitability values across the different structural elements. Such uncertainty entails that deliberately selected transect locations instead of random sampling should be used to account for reach habitat heterogeneity when sample size is small. In that way, Bovee (1997) advised that transects should be placed according to the most random microhabitat variable in the stream, which is usually cover. Moreover, uncertainty in WUA curves significantly decreased when we performed the simulations with channel index 2, which was developed by merging categories providing similar functionality to habitat selection. More channel index partitioning led to a higher uncertainty in WUA magnitude at any BS size resulting from increased variability in SI scores and thus WUA being computed from fewer data points in the hydraulic sample (increased variability in the number of cells presenting zero or very low channel index SI scores), i.e. from reduced sample size, as noted by Gard (2005). Thus, when using a channel index 2-type suitability curve in the habitat simulations, uncertainty around WUA curves may be relatively low even at small BS sizes and simulation results regarded as reliable.

The shape of WUA curves was also highly uncertain at small BS sizes, especially for adult trout. The levels of uncertainty in peak flow observed in our study greatly differ from those estimated by Gard (2005) for juvenile and adult rainbow trout. The confidence intervals for peak flow estimated in our study for adults were significantly wider than those calculated by Gard, whereas it was quite the opposite regarding juveniles. In contrast, our results are within the ranges reported by Williams (2010) at similar sample sizes. Yet HSC variability generated less uncertainty in peak flow than sampling issues when error sampling within transects are considered (Williams, 2010). Changes in the shape of the WUA curves were principally induced by changes in the shape of the water velocity curves, especially

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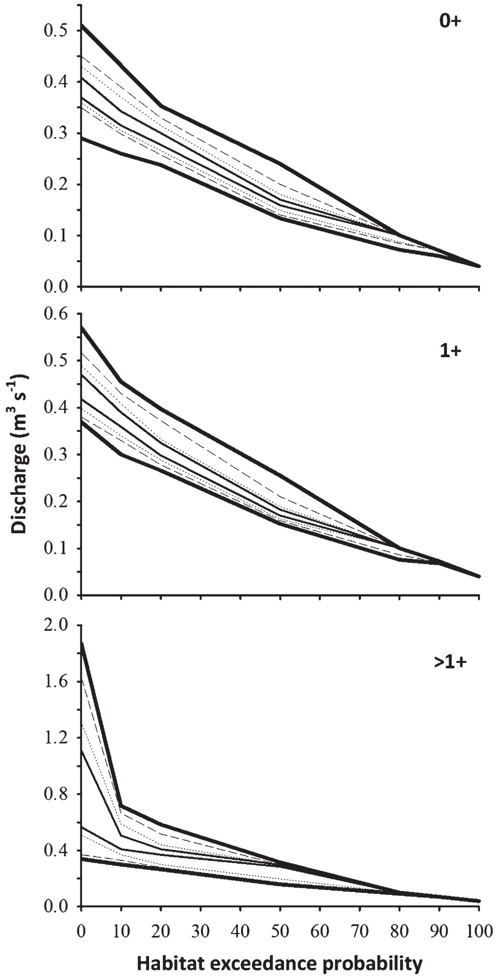

Figure 4. Bootstrap 95% confidence intervals for discharges corresponding to each habitat exceedance probability based on bootstrap samples of 90% (40 transects; inside thin solid line), 75% (33), 50% (22), and 20% (nine; outside thick solid line) of the full set of 44 transects for 0+, 1+ and >1+ age classes.

in adults whose curves were the more variable and shifted from linear to second-order-polynomial models as a function of transect and habitat use observation sample size. These shape shifts may pose additional modelling difficulties because the shape of HSC strongly affects hydraulic simulation errors even in 2-D models (Waddle, 2010).

Nevertheless, implications for water resource management derived from those results may not be as stark as they may appear at first sight. This fact was evidenced more clearly through the habitat time series analyses and derived habitat duration curves. Although the elevation (magnitude) of the habitat duration curves was highly uncertain, the uncertainty in the shape of the curves fell within tolerable limits. Consequently, the uncertainty in the flow associated with different habitat exceedance percentiles was low even at small BS sizes (except at the lowest exceedance probabilities at maximum WUA). However, the bulk of such uncertainty in peak flow for juveniles and especially adults resulted from the shape of the WUA curves being rather constant from a certain flow threshold. As a matter of fact, despite the considerable width of the confidence intervals for the peak flow, the linked variation in maximum WUA was only 5.0 and 3.1% (expressed as the 95% confidence limits on the mean WUA) for juvenile and adult trout, respectively. Therefore, the functional consequences of such high uncertainties around peak flow for either the analysis of alternatives under the IFIM or standard setting purposes using the peak of the WUA curve are negligible. What is more, the uncertainty in the flow values corresponding to other habitat exceedance percentiles (e.g., 50th, 80th or 90th), typically used to recommend instream flow regimes when there is no biological sense in picking the peak flow for that purpose, was insignificant or non-existent even at the smallest BS size.

At this point, the crucial question raised by Payne *et al.* (2004) and Gard (2005) is to define the minimum sample size to obtain simulation results acceptable for reasonable decision-making. Because uncertainty in associated low flows varies with habitat exceedance probability, minimum sample size depends on the habitat limitation levels set to address instream flow needs. Should the 80 or 90% habitat exceedance value be used to define recommended low flows, the lowest BS size (nine transects) would be enough to achieve reliable results. A larger number of transects, 16 or 22, would be necessary if the maximum acceptable width of the confidence interval for peak flow was set to the 25 or 10%, respectively, of the mean for all age classes. If the intended purpose of the instream flow study is to quantify habitat differences between alternative flow conditions, uncertainties in the shape of WUA curves can be critical and should be minimized. To reduce uncertainty around normalized WUA values down to the 25% of the mean, at least 16 transects should be used. In addition, there are many cases where the absolute magnitude of the metrics extracted from the habitat time series are important for modelling population dynamics (e.g. Cheslak & Jacobson, 1990; Cardwell *et al.*, 1996; Capra *et al.*, 2003; Gouraud *et al.*, 2008; Parra *et al.*, 2011) or defining population spatial requirements (e.g. Ayllón *et al.*, 2010b). In those cases, transect number could range between 16 and 33, depending on whether the goal was to be within the 50 or 25% of the true population mean of habitat duration curves, for example. In general, the number of transects required for HSC development to obtain reliable PHABSIM results are within the ranges reported by Payne *et al.* (2004) and Gard (2005) for accurate habitat modelling.

To sum up, the variability around HSC when developed from small BS size involved uncertainties in both WUA magnitude and peak flow similar to those arising from

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selection of the number and location of transects to represent the stream reach. Nevertheless, the uncertainty in WUA values could be reduced down to acceptable levels by using general functional channel index categories like those described by Ayllón *et al.* (2010a). A more precise description of substrate and cover preferences (e.g. Ayllón *et al.*, 2009) could be used when time or budget constraints do not limit sampling effort. Results also highlighted that high levels of uncertainty do not necessarily entail critical errors in the decision-making process. The next step would involve estimating the total uncertainty resulting from the transect selection and HSC together and determining the nature of their interactive effects (additive vs non-additive). Further, confidence intervals for distribution of WUA results over time could be estimated by taking into account the existing uncertainty around hydrologic metrics (Kennard *et al.*, 2010). Finally, future research should also focus on estimating total uncertainty around WUA curves at different river reach typologies, in which both HSC (e.g. Ayllón *et al.*, 2010a) and required transect sample size (Payne *et al.*, 2004) are known to vary across, in order to provide a guidance for selecting the number of transects required to minimize errors based on modelling results in future instream flow studies or other PHABSIM applications.

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