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EVALUATING METHODS TO ESTABLISH HABITAT SUITABILITY CRITERIA: A CASE STUDY IN THE UPPER DELAWARE RIVER BASIN, USA

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ABSTRACT

Defining habitat suitability criteria (HSC) of aquatic biota can be a key component to environmental flow science. HSC can be developed through numerous methods; however, few studies have evaluated the consistency of HSC developed by different methodologies. We directly compared HSC for depth and velocity developed by the Delphi method (expert opinion) and by two primary literature meta-analyses (literature-derived range and interquartile range) to assess whether these independent methods produce analogous criteria for multiple species (rainbow trout, brown trout, American shad, and shallow fast guild) and life stages. We further evaluated how these two independently developed HSC affect calculations of habitat availability under three alternative reservoir management scenarios in the upper Delaware River at a mesohabitat (main channel, stream margins, and flood plain), reach, and basin scale. In general, literature-derived HSC fell within the range of the Delphi HSC, with highest congruence for velocity habitat. Habitat area predicted using the Delphi HSC fell between the habitat area predicted using two literature-derived HSC, both at the basin and the site scale. Predicted habitat increased in shallow regions (stream margins and flood plain) using literature-derived HSC while Delphi-derived HSC predicted increased channel habitat. HSC generally favoured the same reservoir management scenario; however, no favoured reservoir management scenario was the most common outcome when applying the literature range HSC. The differences found in this study lend insight into how different methodologies can shape HSC and their consequences for predicted habitat and water management decisions. Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: flow management; habitat assessment; Delphi panel; IFIM; environmental flows; trout; shad

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INTRODUCTION

One of the most highly contentious resources worldwide is fresh water. Demand for this limited natural resource is rapidly increasing with human population growth, and water availability issues are exacerbated by unsustainable water management practices and climate variability (Baron *et al.*, 2002). This demand has resulted in an alteration to instream flows of many rivers. Minimum flow values have historically been used to balance instream flows and human water demands; however, it is now widely accepted that minimum flow recommendations are not successful in protecting the diversity of human and ecological flow needs (Poff *et al.*, 1997; Poff, 2009; Poff and Zimmerman, 2010). Environmental flow science, on the other hand, attempts to balance

diverse human water needs with the natural flows necessary to support aquatic biota and their associated ecological processes (Poff *et al.*, 2010). However, developing comprehensive flow management strategies that incorporate a variety of interacting biotic and abiotic variables can be challenging.

One approach to evaluate the effects of altered hydrologic regimes is to model habitat conditions for key species in specific reaches of river using the Instream Flow Incremental Methodology (IFIM). A key component to this approach within environmental flow science is to understand the habitat needs of biota—the environmental conditions suitable for each species—also known as habitat suitability criteria (HSC) (Bovee, 1986). Defining HSC for individual species can be challenging because habitat requirements vary by life stage, season, and drainage basin and can also be altered by multiple interacting environmental variables (Orth, 1987). Similarly, the upper and lower bounds of HSC depend on the criterion used to define what is ‘suitable’ (e.g. tolerable

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versus optimal versus preferred). Once established, HSC can be incorporated into a framework for assessing environmental flows, such as IFIM, whereby HSC are linked to modelled or measured habitat at a relevant scale (e.g. 1 m² pixels) and used to quantify the total amount of suitable habitat for a given species or guild (Bovee *et al.*, 1998; Tharme, 2003).

Several approaches have been used to define HSC for individual species or guilds including empirical investigation (experimentation and field surveys), literature meta-analysis, and expert opinion (Bovee, 1986; Brooks, 1997). Each method for deriving HSC has strengths and weaknesses. Experimental studies can isolate the effects of individual variables on species response but are often over-simplified and may not reflect field conditions (Diamond,). Field surveys derive HSC from areas where species are observed, but are dependent on timing and conditions of the survey, total habitat area available, and may not represent the full extent of habitat used by the species (Bovee, 1986; Conklin *et al.*, 1996; Vismara *et al.*, 2001; Ahmadi-Nedushan *et al.*, 2006). Literature analyses present a summary of the scientific data available for a given species, but can be limited in quantity or scope depending on the species of interest (Bovee, 1986). Professional opinion approaches (e.g. Delphi method) rely on those most knowledgeable to define species habitat needs; however personal, geographical, or cognitive biases may influence the accuracy of this HSC approach (Bovee, 1986; Leclerc *et al.*, 2003). Because many approaches to environmental flow science rely heavily on HSC, it is necessary to understand how the resulting HSC produced via these various approaches compare and how they affect estimates of predicted available habitat.

The purpose of the current study was to compare HSC developed via the Delphi method to those derived from a literature meta-analysis and to investigate differences in modelled habitat predictions based on these HSC. We used the Delaware River basin as a case study and tested how each set of HSC would affect calculations of potentially available habitat at three scales (basin, site, and within-site mesohabitat) using a previously published decision support system for this area (Maloney *et al.*, 2015). We also examined how each set of HSC would affect the favourability (defined as maximal predicted habitat) of three alternative reservoir management scenarios that have been applied in the basin. Specifically, the present HSC analysis addressed three questions: (i) Were Delphi method HSC congruent with the literature? (ii) If there were differences in predicted habitat between the Delphi and literature HSC, where do these occur across geographical scales? (iii) Do literature-derived HSC result in the same management decisions as Delphi HSC?

METHODS

Study site

The Delaware River basin, USA, is managed according to a 1954 Supreme Court Decree (and subsequent negotiated revisions) to support multiple competing water needs including recreation, saltwater repulsion, flood mitigation, and federally endangered species (Delaware Decree Parties, 2013). To assist managers in evaluating flow scenarios and their effects on key aquatic species within the Delaware River basin, Bovee *et al.* (2007) developed the upper Delaware River Decision Support System (DRDSS) which has since been modified and renamed the Riverine Environmental Flow Decision Support System (REFDSS; Maloney *et al.*, 2015). The REFDSS is based on an IFIM framework and incorporates depth and velocity HSC with hydrologic and hydrodynamic models to quantify potential habitat for a suite of species and life stages ('species/life stage combinations' hereafter; Table I) at 11 sites in the upper Delaware River basin, 3 of which lie within the Upper Delaware Scenic and Recreational River (Figure 1). For a full description of the mechanics behind the REFDSS refer to Bovee *et al.* (2007), Maloney *et al.* (2015), and Talbert *et al.* (2014).

Literature meta-analysis

Habitat suitability criteria for depth and velocity were originally characterized in the DRDSS and the REFDSS using the Delphi method whereby a panel of six stakeholder-selected experts determined the minimum and maximum suitable depth and velocity values for each of the key species/life stage combinations for the Delaware River basin (Bovee *et al.*, 2007; Table I). We compared these Delphi-derived HSC to values obtained from a comprehensive primary literature review that included experimental and field studies. Only peer-reviewed scientific articles were used in this meta-analysis; gray literature, reports, theses, or secondary literature were excluded from this review. Major search engines included Web of Knowledge, Google Scholar, and U.S. Geological Survey Digital Desktop Library. Search terms included common and scientific names or guild names in conjunction with the following terms: depth, velocity, flow, habitat, habitat suitability, juvenile, spawning, reproduction, and incubation. Data obtained for guilds (shallow-fast and shallow-slow) were limited to the species outlined in Bovee *et al.* (2007).

A given article was included in the meta-analysis if it presented either depth or velocity data (either some metric of central tendency—e.g. mean or median, or extreme values—e.g. minimum and maximum) in a given study where the species of interest were observed. Life stages (adult, juvenile, etc.) of the species were generally specified in the

Table I. Habitat suitability criteria (HSC) for depth in metres (a) and velocity in metres per second (b) for nine species/life stage combinations in the upper Delaware River, USA

(a)	Species	Life stage	Delphi depth (m)	Lit range depth (m)	Lit IQR depth (m)	Total N	% within Delphi range
	Brown trout (<i>Salmo trutta</i>)	adult	0.3–100	0.05–54.00	0.15–0.59	131	53.44
		juvenile	0.2–0.8	0.05–1.50	0.13–0.38	183	56.28
		spawning	0.2–0.6	0.05–0.52	0.20–0.40	52	84.62
		incubation	0.2–1.0	0.05–0.52	0.18–0.32	33	72.73
	Rainbow trout (<i>Oncorhynchus mykiss</i>)	adult	0.3–100	0.07–37.90	0.21–1.20	60	70.00
		juvenile	0.2–1.0	0.12–1.70	0.32–0.63	39	82.05
	American shad (<i>Alosa sapidissima</i>)	spawning	0.3–3.0	0.2–7.30	1.39–4.11	23	47.83
		juvenile	0.25–1.6	0.2–11.00	1.00–4.80	15	40.00
	Shallow-slow guild*		0.05–0.3	N/A	N/A	0	100
	Shallow-fast guild†		0.05–0.3	0.1–1.00	0.17–0.48	18	66.67
(b)	Species	Life stage	Delphi Vel (m/s)	Lit range Vel (m/s)	Lit IQR--Vel (m/s)	Total N	% within Delphi range
	Brown trout (<i>Salmo trutta</i>)	adult	0.0–1.0	0.02–1.05	0.13–0.43	80	96.25
		juvenile	0.0–0.7	0.00–1.05	0.11–0.36	100	95.00
		spawning	0.3–0.8	0.10–1.08	0.29–0.50	55	70.91
		incubation	0.15–1.2	0.06–1.08	0.31–0.47	33	93.94
	Rainbow trout (<i>Oncorhynchus mykiss</i>)	adult	0.0–1.2	0.00–0.91	0.06–0.21	25	100.00
		juvenile	0.0–0.8	0.00–1.39	0.04–0.23	43	93.02
	American shad (<i>Alosa sapidissima</i>)	spawning	0.2–0.7	0.01–1.10	0.41–0.61	19	78.95
		juvenile	0.0–0.6	0.00–1.02	0.10–0.58	12	83.33
	Shallow-slow guild*		0.0–0.3	N/A	N/A	1	50.00
	Shallow-fast guild†		0.3–1.2	0.09–0.60	0.16–0.46	8	62.50

Delphi, HSC developed by the expert opinion Delphi method and reported in Bovee *et al.* (2007); *Lit range*, literature-derived HSC for either depth or velocity including all literature observations; *Lit IQR*, interquartile range of literature observations for either depth or velocity (refer to text for details); *Total N*, total number of observations in the literature for a given species/life stage combination; *% within Delphi range*, percentage of literature values that fell within Delphi HSC.

*Bridle shiner (*Notropis bifrenatus*), blue spotted sunfish (*Enneacanthus gloriosus*), eastern mudminnow (*Umbra pygmaea*), and cutlips minnow (*Exoglossum maxillina*); refer to Bovee *et al.* (2007)

†Margined madtom (*Noturus insignis*), juvenile fallfish (*Semotilus corporalis*), and American eel (*Anguilla rostrata*); refer to Bovee *et al.* (2007)

literature itself, but were occasionally vague, especially for trout. In these instances (e.g. when only age data were reported), trout ≥ 2 years of age were considered to be adults and younger than 2 years were considered to be juveniles. Data from multiple sites or years reported within the same study were included as separate observations in our analysis. Total number of data points for analysis varied depending on the amount of published literature available on each species or guild (Table I, Supplemental Table 1). All literature values were used to calculate the minimum and maximum depth and velocity for each species/life stage combination. Two literature-based HSC were established for both depth and velocity for comparison to those developed by the Delphi method: total range and interquartile range (IQR). The total range included all literature-extracted data points and was therefore used to represent the total tolerable habitat (tolerance limits) for a given species. To capture the notion of 'optimal' and/or 'preferred' habitat, we calculated the boundaries of the IQR (data between 25th and 75th percentiles) of all literature values for both depth and velocity and used these as the upper and lower HSC limits (Thomas and Bovee, 1993). To determine the congruence between the

literature-derived and Delphi-derived depth and velocity values, we calculated the percent of literature values that fell within the Delphi ranges for each species/life stage combination.

Comparing the predicted habitat generated under the Flexible Flow Management Plan for each set of HSC

The REFDSS currently incorporates three alternative reservoir management scenarios: Rev1, Rev7, and Flexible Flow Management Plan (FFMP), explained in detail in Maloney *et al.* (2015). Briefly, Rev1 represents an early attempt to manage flows to reduce thermal issues in the river, with Rev7 being a subsequent temporary revision incorporating drought management, and FFMP being a more comprehensive approach that also includes, among other things, dedicated storage to protect instream flow habitat. To evaluate how the Delphi and literature-derived HSC would affect predicted habitat, we imported the three sets of HSC (Delphi HSC, literature total range HSC, and literature IQR HSC) into the REFDSS (v.1.1.3) for each species/life stage combination. The REFDSS was then used to calculate a composite

Figure 1. Map of study sites (filled circles) modelled in the Riverine Environmental Flow Decision Support System (REFDSS; Maloney *et al.*, 2015), cities (triangles), and dams (stars) in the upper Delaware River, USA

habitat area (the total area found suitable for both depth and velocity values; Maloney *et al.*, 2015), on a yearly basis for the entire period of record (1929–2000) at a basin-wide scale (across all 11 sites). The amount of predicted habitat basin-wide was compared under the different HSC by plotting total habitat area for each year using the Delphi HSC against total habitat area using the literature-derived HSC. For simplicity, this was completed using only the most recent reservoir management scenario, FFMP. We followed Bovee *et al.* (2007) and Maloney *et al.* (2015) and highlighted differences in habitat area $\geq 10\%$ from a 1:1 correspondence.

To assess site-scale differences in predicted habitat area, we calculated a proportional change in habitat area for each species/life stage combination at each of the 11 sites in the upper Delaware River (again, only for the FFMP management scenario). For each site and species/life stage combination averaged over the entire period of record, the predicted habitat area calculated by the Delphi method was subtracted

from the predicted habitat area calculated using each of the literature-derived HSC and divided by the total wetted area of each site $\left[\frac{(\text{Lit-derived habitat area} - \text{Delphi habitat area})}{\text{Total wetted area}} \right]$. Negative values suggested lower predicted habitat while positive values suggested a higher predicted habitat relative to the Delphi approach.

Finally, total habitat was separated into four meso-scale habitat categories: flood plain, stream margins, channel, and island. To do so, islands and stream banks were digitized from 2D hydrodynamic modelled depth habitat maps at long-term median discharge levels and confirmed using aerial photographs taken under similar discharge levels in ArcGIS 9.2 (ESRI Redlands, California, USA). Areas outside of the stream banks were dubbed flood plain habitat. Stream margin habitat, or the regions bordering the stream bank, was defined by creating buffers (5% of the mean wetted width of each reach) inside the stream banks and around islands. Channel habitat comprised the remainder of the

stream reach not included in the other three categories. The resultant digitized meso-scale habitat file was imported into the REFDSS, which was recoded to quantify each of the four habitat types for the Delphi and literature-derived HSC. We calculated the proportion of habitat for each meso-scale habitat category relative to the total habitat area predicted by Delphi or literature-derived HSC. We then calculated the difference between Delphi and literature-derived proportional habitat for each category. For example, to quantify the difference in channel habitat predicted by the Delphi and IQR HSC we calculated $\frac{\text{IQR channel habitat}}{\text{IQR total habitat}} - \frac{\text{Delphi channel habitat}}{\text{Delphi total habitat}}$ for each species/life stage combination averaged over the entire period of record. Negative values indicated habitat categories in which Delphi HSC predicted greater habitat while positive values included habitat categories with greater habitat predicted by the literature-derived HSC. Differences $\geq 10\%$ were considered to be a measurable change.

Comparing the favoured reservoir management scenario for each set of HSC

We used basin-wide calculated habitat area from the REFDSS to examine if the competing HSC resulted in different amounts of potentially available habitat for each of two historic (Rev1 and Rev7) and the most recent (FFMP) reservoir management scenario. Each reservoir management scenario was assessed relative to the other two reservoir management scenarios on a yearly basis. Again, deviations $\geq 10\%$ between reservoir management scenarios were considered to be a measurable difference. When a reservoir management scenario resulted in $\geq 10\%$ habitat than the other two scenarios, it was considered to be the favoured reservoir management scenario for that year. The total number of years that each reservoir management scenario was favoured was calculated for each species/life stage combination. If there were no differences $\geq 10\%$ between reservoir management scenarios, then no scenario was favoured for that year. We evaluated the total number of years for which each reservoir management scenario (Rev1, Rev7, FFMP, or no favoured reservoir management scenario) was favoured under the three HSC.

RESULTS

Literature meta-analysis

We extracted 938 depth and velocity observations from a total of 74 articles for the given species/life stage combinations: brown trout, 40 (articles); rainbow trout, 25; American shad, 7; shallow slow guild, 1; and shallow fast guild, 3 (Table I, Supplemental Table 1). Limited primary

literature was available reporting depth or velocity values for shallow-slow and shallow-fast guilds. Because of these data limitations, shallow slow guild was excluded from further analysis. Literature depth and velocities were variable and wide-ranging for all species and life stages (Table I, Supplemental Table 1). With the exception of spawning and juvenile American shad, $>50\%$ of the literature values fell within the Delphi HSC habitat range reported in Bovee *et al.* (2007). A larger percentage of literature velocity values were included in the Delphi range (range of 62.50–100.00%), while depth values identified by the Delphi method were less encompassing of literature values (range of 40.00–84.62%). At the lower depth limits, literature-derived HSC were consistently shallower than the Delphi HSC; at the upper depth limits, the Delphi HSC were substantially greater for adult brown and rainbow trout.

Comparing the predicted habitat generated under the FFMP

Basin-wide, literature-derived range HSC generally predicted greater habitat area ($\geq 10\%$) compared with the Delphi HSC (except for incubating brown trout; Figure 2a). This was especially pronounced for juvenile rainbow and brown trout. Conversely, IQR HSC predicted less habitat area relative to Delphi HSC, particularly for adult brown and rainbow trout and juvenile rainbow trout; slightly more habitat was predicted for shallow fast guild (Figure 2b). Site-scale changes in predicted available habitat relative to Delphi HSC varied by species/life stage combination and HSC (Table II). In general, patterns observed across the entire basin were also reflected at the site scale: literature range values resulted in strictly higher estimates of predicted habitat except for incubating brown trout; IQR values resulted in lower predicted habitat for all species/life stage combinations except shallow fast guild. The site that experienced increases in predicted habitat for the greatest number of species/life stage combinations was WB0 for literature range, with the majority of those differences occurring for brown trout. No clear pattern of losses or gains in predicted habitat within individual sites was observed using the literature-derived IQR HSC.

For all species combined, there were no differences in predicted habitat area $\geq 10\%$ between the Delphi method and literature-derived HSC in any of the four habitat categories (Figure 3a). For individual species/life stage combinations, the Delphi HSC generally predicted greater amounts of channel habitat than did the literature-derived HSC for individual species/life stage combinations (Figure 3b,c,d,e,f,g); increases in flood plain and stream margin habitat were typically observed using the literature-derived HSC (Figure 3b,c,e,f,g). However, these patterns were not ubiquitous

Figure 2. Relationship between total predicted habitat area (ha) under the FFMP reservoir management scenario using the Delphi-derived habitat suitability criteria (HSC) reported in Bovee *et al.* (2007) and literature-derived HSC: Literature range, HSC including all literature observations (a); Literature IQR, HSC including the interquartile range of all literature observations (b). Individual points represent predicted habitat area for a single year (1929–2000) for each of nine species/life stage combinations. Solid lines indicate a 1:1 relationship and dashed lines represent $\pm 10\%$ around the 1:1 line

across all species/life stage combinations. Shallow fast guild had the most dramatic differences in predicted habitat between Delphi and literature-derived HSC where the literature HSC predicted more channel habitat and the Delphi HSC predicted greater stream margin and flood plain habitat (Figure 3j). Island habitat never differed greater than 10% between HSC, and there were no differences in any habitat categories between the HSC for either of the shad life stages (Figure 3h,i).

Comparing the favoured reservoir management scenario for each set of HSC

During most years, habitat predicted under the three reservoir management scenarios did not differ by $\geq 10\%$ resulting in no favoured reservoir management scenario for each species/life stage combination and all species

combined; however, there were a few exceptions. FFMP was favoured in most years for incubating brown trout (IQR and Delphi; Figure 4e) and spawning shad (IQR; Figure 4i) and Rev7 was favoured in most years for spawning brown trout (IQR; Figure 4d). The 'no reservoir management scenario' option was most frequently observed when using the literature-derived range HSC compared with the Delphi or IQR (Note that the 'no reservoir management scenario' option is not explicitly depicted in Figure 4 for ease in distinguishing between the other three reservoir management scenarios). Of the three remaining reservoir management scenarios, FFMP was the most frequently favoured scenario for all species/life stage combinations except for spawning brown trout where Rev7 was most common for all HSC (Figure 4d) and adult brown trout where Rev7 was also most common, but only for IQR (Figure 4b).

Table II. Proportion of total wetted area of predicted habitat change (ha) calculated under the FFMP reservoir management scenario from the literature-derived habitat suitability criteria (HSC) relative to those calculated by the Delphi method (Bovee *et al.*, 2007) at 11 sites in the upper Delaware River, USA for nine species/life stage combinations averaged over the entire period of record (1929–2000)

Sites		Brown trout adult	Brown trout juvenile	Brown trout spawning	Brown trout incubation	Rainbow trout adult	Rainbow trout juvenile	American shad Juvenile	American shad spawning	Shallow fast guld
Delphi versus lit range	Del1	0.16	0.54	0.08	-0.19	0.23	0.42	0.18	0.46	0.40
	Del2	0.15	0.37	0.07	-0.12	0.12	0.43	0.25	0.42	0.16
	Del3	0.24	0.47	0.09	-0.21	0.22	0.46	0.21	0.44	0.27
	WB0	0.57	0.53	0.43	0.33	0.56	0.36			0.34
	WB1	0.38	0.48	0.23	-0.04	0.40	0.34			0.39
	EB0	0.32	0.40	0.30	0.15	0.42	0.24			0.40
	EB1	0.11	0.42	0.14	-0.10	0.25	0.27			0.38
	EB2	0.25	0.49	0.12	-0.22	0.27	0.49	0.16	0.43	0.27
	NVR0	0.31	0.39	0.29	0.11	0.39	0.21			0.45
	NVR1	0.38	0.38	0.32	-0.12	0.41	0.20			0.57
	NVR2	0.34	0.43	0.28	0.02	0.37	0.30	0.20	0.43	0.31
Delphi versus lit IQR	Del1	-0.57	-0.29	-0.08	-0.34	-0.57	-0.41	-0.51	-0.41	0.05
	Del2	-0.57	-0.17	-0.06	-0.21	-0.60	-0.23	-0.32	-0.26	0.01
	Del3	-0.48	-0.21	-0.09	-0.30	-0.52	-0.31	-0.43	-0.32	0.03
	WB0	-0.13	-0.22	-0.06	-0.17	-0.25	-0.31			0.03
	WB1	-0.34	-0.35	-0.11	-0.37	-0.44	-0.46			0.05
	EB0	-0.18	-0.32	-0.03	-0.25	-0.29	-0.47			0.13
	EB1	-0.51	-0.41	-0.05	-0.30	-0.44	-0.49			0.05
	EB2	-0.45	-0.21	-0.06	-0.32	-0.44	-0.32	-0.51	-0.30	0.03
	NVR0	-0.31	-0.47	-0.05	-0.31	-0.34	-0.55			0.04
	NVR1	-0.20	-0.52	-0.05	-0.44	-0.21	-0.61			0.10
	NVR2	-0.25	-0.30	-0.09	-0.38	-0.35	-0.44	-0.44	-0.24	0.01

Negative values (red) indicate a lower proportion of predicted habitat relative to the Delphi method ($\geq 10\%$ difference); positive values (green) indicate a higher proportion of predicted habitat relative to the Delphi method ($\geq 10\%$ difference).

DISCUSSION

While there were substantial areas of overlap between Delphi and literature-derived HSC for most species/life stage combinations, some consistent and important differences were found in HSC generated using the different methodologies. Delphi-estimated velocities had stronger literature support than depth estimates; this was primarily because of the panel's exclusion of shallow water (< 0.3 m) in their estimates of suitable depth and substantially higher upper depth limits for adult trout species. The species/life stage combinations with the lowest agreement occurred for depth between the Delphi and literature methods for both life stages of shad, potentially as a function of limited data for these species (23 observations or less). Future research on the habitat preferences for this species is necessary to either support or refute the estimates of the Delphi panel and literature-derived HSC. There was also poor literature support for the Delphi-defined depth habitat for the two most highly studied species/life stage combinations, adult and juvenile brown trout. This could have been because of a variety of methodological biases discussed in the succeeding texts. Nonetheless, depth has been suggested to be more important than velocity in defining HSC for trout (Vismara *et al.*, 2001). Therefore, accurate depth estimates, including

empirical data collected specifically within the Delaware River basin, are needed to increase confidence in predicted habitat and may distinguish which set of HSC are most reflective of the true habitat use of these species.

Predicted habitat area generated from the REFDS was vastly different for all HSC: IQR predicted the least amount of habitat, followed by the Delphi HSC, and the literature range predicted the greatest amount of habitat. The broadest range of conditions, in which an organism can survive, defines its tolerance limits; presumably, the literature-derived range HSC served as a proxy for these boundaries (Willmer *et al.*, 2005). The area of highest habitat quality, or optimal habitat, defines the locations where an organism is most likely to experience maximal physiological or reproductive condition (Willmer *et al.*, 2005). In this study, we used the literature-derived IQR as a proxy for optimal habitat, although we have no way to verify the extent to which this is true.¹ Nonetheless, the breadth of HSC used in environmental flow modelling, like the REFDS, needs to be based

¹It should be noted that this is overly simplistic as both tolerance, and optimal habitat limits are likely more complex, varying by season, environmental history, etc.

Figure 3. Proportional difference in habitat area between Delphi-derived habitat suitability criteria (HSC) and literature-derived HSC for nine species/life stage combinations and summed across all modelled species. Four meso-scale habitat regions are depicted: flood plain (black), stream margin (light gray), channel (white), and island (dark gray). Negative values indicate regions with greater predicted habitat using the Delphi HSC; positive values indicate greater predicted habitat for the literature-derived HSC. Asterisks indicate differences $\geq 10\%$

on the managers' desired sensitivity. The current REFDDSS utilizes the Delphi-derived HSC in which panel members were asked to delineate 'suitable' habitat. Where this falls along the spectrum between 'tolerance' and 'optimality' is unclear. The habitat predicted using the Delphi HSC was between literature-derived proxies for optimal and tolerable; this could have been because of the Delphi-method itself,

which iteratively removes outlying observations until consensus is reached. The desired degree of habitat suitability needs to be clearly specified to Delphi panel members so that the final HSC serve their intended use. Alternatively, degrees of habitat suitability could be incorporated into more complex HSC (e.g. histograms, probability curves, and multivariate analyses) that could reflect tolerable and

Figure 4. Proportion of years (1929–2000) for which each reservoir management scenario (Rev1, Rev7, and FFMP) was favoured ($\geq 10\%$ difference in predicted habitat) for nine species/life stage combinations and summed across all modelled species using one of three habitat suitability criteria (HSC): HSC developed using the Delphi method (Bovee *et al.*, 2007); literature-derived HSC including all observations (Lit range); and interquartile range of literature observations (Lit IQR). Note that the 'no reservoir management scenario' option is not explicitly depicted for ease in distinguishing between the other three reservoir management scenarios. However, the data are proportional, and therefore, the 'no reservoir management scenario option' represents the difference between 1 and the sum of the three reservoir management scenarios.

optimal habitat simultaneously (Bovee, 1986; Ahmadi-Nedushan *et al.*, 2006). A more simplistic but potentially useful approach would be to use both a liberal and a conservative set of HSC for all potential reservoir management scenarios to determine how robust they are to differences in HSC. Again, the differences between the predicted habitat

using the various HSC will ultimately depend on the model into which they are incorporated.

Differences in predicted habitat area at the site scale predicted by the various HSC were similar to those predicted at the basin scale (increased habitat with literature-derived range and decreased habitat with literature IQR). Unusually

large gains in predicted habitat relative to the Delphi-predicted habitat estimates were evident at site WB0 (particularly for trout). The reason for these differences is unclear but may be worth further investigation if this is a site of particular interest to managers. The differences among the HSC in predicted meso-scale habitat are likely a reflection of the biases inherent within each of the HSC methods. Upper velocity and depth extremes are most likely underrepresented in the literature as a function of field conditions that are most conducive to sampling (i.e. low to moderate depths and velocities; Vismara *et al.*, 2001). Literature-derived HSC incorporated shallower depths compared with Delphi-derived HSC potentially as a reflection of this bias. This yielded increases in stream margin and flood plain habitat using the literature and increases in deeper channel habitat using Delphi HSC. Additionally, unintentional panel bias (Leclerc *et al.*, 2003) may be responsible for the differences between the Delphi and literature-derived HSC. For example, panel members may have envisioned 'adult' trout as primarily large trophy trout rather than our narrower definition based on reproductive capability.

While differences in predicted habitat area depended on HSC, how these differences translated into management outcomes was dependent upon the competing reservoir management scenarios (Rev1, Rev7, and FFMP) in the Delaware River and the mechanics of the REFDSS (Bovee *et al.*, 2007; Maloney *et al.*, 2015). Differences between competing reservoir management scenarios were indistinguishable in general, but particularly when literature-range HSC were incorporated into the REFDSS. These results highlight the small actual differences in modelled flow between the three reservoir management scenarios used in the REFDSS (Supplemental Fig. 1). When a reservoir management scenario was preferred, however, FFMP tended to be favoured for all HSC. The HSC predicting less habitat area (IQR and Delphi) allowed for the detection of these small differences in reservoir management scenarios. The increased amount of predicted habitat generated using the literature-derived range HSC resulted in so much predicted habitat that differences between reservoir management scenarios were masked. Therefore, management outcomes may be dependent on what HSC are used. This further supports the need for a range of HSC in assessing competing management scenarios; confidence in any scenario would be greater if it was favoured under all available criteria, as FFMP was in this study.

Along with potential biases to all HSC methods, there are additional limitations to, and assumptions made in, this study. First, the data used in this study represent only primary scientific literature and do not reflect the vast amount of data published as gray literature. While we feel that this limited our analysis to the most rigorously vetted data, large data gaps do exist in the literature (in this case, for

both guilds and shad), and gray literature may provide a suitable alternative. Similarly, the primary literature that could be used for this study was limited by the number of published articles reporting the *exact type* of data needed (minimum, maximum, and mean or median depth and/or flow values). Many meticulous studies of habitat suitability were excluded from this analysis because they did not report the necessary data. These data gaps (in both the number of publications and the data required from the publications) highlight needed research to develop the most comprehensive HSC and thereby ecological flow models. Secondly, it is likely that we missed articles, particularly papers in obscure or unavailable journals. Finally, we made the assumption that depth and velocity tolerances were not basin- or stream size- specific, as the results reported here summarize data from throughout the USA and Europe. While some have argued that site-specific HSC are more advantageous for a given river (Heggenes and Saltveit, 1990; Vismara *et al.*, 2001; Strakosh *et al.*, 2003), there are not enough published data on habitat suitability for the Delaware River alone to define comprehensive HSC and collecting field data is time-consuming and costly. While the literature-derived HSC are not Delaware River specific, our approach provides a starting point, the applicability of which could be tested in this and other systems (Thomas and Bovee, 1993; Guay *et al.*, 2003).

These results illustrate how different methodologies (Delphi and literature) used to define HSC can portray instream habitats under different flow regimes in highly divergent ways. Whatever methodology is used, it is necessary to clearly define the end criteria (tolerance versus optimal) for the species of interest to ensure that management decisions are based on the desired degree of habitat suitability. This study also indicates that multiple HSC collected using a variety of methods should be compared to verify their validity and potentially combined to build confidence in the modelled habitat output. Our ability to adequately define HSC ultimately impacts the accuracy of the ecological flow models in which they are incorporated, thereby influencing environmental flow prescriptions.

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