Received: 6 January 2016 | Revised: 1 December 2016 | Accepted: 4 December 2016
DOI: 10.1002/eco.1823

WILEY

RESEARCH ARTICLE

Projecting impacts of climate change on habitat availability in a macrophyte dominated Chalk River

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Abstract

Climate change will impact fluvial ecosystems through changes in the flow regime. Physical habitat is an established measure of a river's ecological status when assessing changes to flow. Yet, it requires extensive datasets, is site specific, and does not account for dynamic processes; shortcomings that the use of hydrological and hydraulic models may alleviate. Here, simulated flows along a 600 m reach of the River Lambourn, Boxford, UK, were extracted from the 1D MIKE 11 hydraulic component of an integrated MIKE SHE model of the Centre for Ecology & Hydrology River Lambourn Observatory. In-channel seasonal macrophyte growth and management through cutting alter water levels, represented in the hydraulic model by manipulating channel bed roughness (Manning's n). Assessment of climate change used outputs from the UK Climate Projections 2009 ensemble of global climate models for the 2080s. River discharge outputs were disaggregated to provide velocity and depth profiles across 41 cross sections along the reach. These were integrated with habitat suitability criteria for brown trout (*Salmo trutta*) to generate a measure of available physical habitat. The influence of macrophyte growth caused the habitat-discharge relationship to be unusable in evaluating the sensitivity of brown trout to flow changes. Instead, projected time series were used to show an overall reduction in habitat availability, more for adult than juvenile trout. Results highlighted the impact of weed cutting, and its potential role in mitigating both flood risk and the ecological impacts of climate change. The use of a hydraulic model to assess physical habitat availability has worldwide applicability.

KEYWORDS

climate change, ecohydrology, hydrological and hydraulic modelling, physical habitat, river management

1 | INTRODUCTION

Unequivocal warming of the climate (IPCC, 2014) will impact the global hydrological cycle (Arnell & Gosling, 2013), with implications for aquatic ecosystems (Matthews & Quesne, 2009; Poff, Brinson, & Day, 2002) and water resources (Gosling, Warren, Arnell, Good, & Caesar, 2011; Oki & Kanae, 2006). Climate change will alter the magnitude as well as the temporal and spatial distribution of precipitation and evapotranspiration, which, in turn, will result in changes to runoff and river-flow regimes. The importance of flow regime in controlling processes of water quality, sediment transport, dissolved oxygen concentrations, and the type and distribution of habitat (Bunn & Arthington, 2002; Poff et al., 1997; Richter, Baumgartner, Braun, & Powell, 1998; Warren, Dunbar, & Smith, 2015) means that climate change is likely to have major impacts on fluvial ecosystems, their biota, and the many services that they provide.

A direct relationship between physical habitat and flow enables assessments of the ecological responses to changes in the flow regime (Beecher, Johnson, & Carleton, 1993; Cavendish & Duncan, 1986). Flow in this sense is used as a proxy for water depth and velocity, as these provide physical habitat for plants, invertebrates, and fish through interactions between the flow rate and channel morphology (Gallagher & Gard, 1999; Gore, Crawford, & Addison, 1998; Jowett, 1992; Jowett, Richardson, & Bonnett, 2005). Hydraulic changes due to climate change may be linked to the depth and velocity requirements for different species and provide a measure of available physical habitat as a function of flow.

The physical habitat simulation (PHABSIM) system was the first modelling framework to quantify physical habitat for a specific discharge as a combined function of depth, velocity, and substrate or cover (Bovee, 1978; Bovee, 1982; Bovee, Lamb, Bartholow, Stalnaker, & Taylor, 1998). The method is well suited to scenario analysis; the slope of the physical habitat-discharge relationship that is a key output of PHABSIM defines habitat sensitivity to change in flow. The steeper the curve the greater the sensitivity to flow. This approach is a legal requirement for many impact studies in the USA (Reiser, Wesche, & Estes, 1989) and has been standard use by the Environment Agency of England and Wales for determining sensitivity of rivers to abstraction, a requirement for catchment abstraction management strategies (Dunbar et al., 2002), and assessing ecological status for the European Water Framework Directive (Acreman et al., 2006). Despite criticisms of an insufficient link between habitat and biomass (Mathur, Bason, Purdy, & Silver, 1985; Orth & Maughan, 1986), models built on a similar concept have also been applied worldwide (Dunbar & Acreman, 2001), including RHYbasiM in New Zealand (Jowett, 1989), RSS in Norway (Killingtviet & Harby, 1994), EVHA in France (Ginot, 1995), HABIOSIM in Canada (Dunbar et al., 1997b), and CASiMIR in Germany (Eisner, Young, Schneider, & Kopecki, 2005; Jorde, 1996). However, in application, physical habitat modelling is site specific and resource intensive (Tharme, 2003). It requires extensive collection of field data at several different flows (Bovee, 1982) to obtain a physical habitat-discharge relationship. Approaches based on defining habitat-discharge relationships from fewer and/or simpler measurements of catchment, hydraulic or morphological characteristics (Booker & Acreman, 2007; Klaar et al., 2014; Lamouroux & Capra, 2002; Lamouroux & Jowett, 2005; Souchon & Capra, 2004), have had limited success and remain suited for broad-scale screening exercises only. Additionally, alterations to the river that affect the parameters of depth and velocity are not accounted for. These may include instream macrophyte growth, groundwater exchange, or morphological adjustment that are key features of many dynamic systems. Indeed, the influence of macrophytes on physical habitat was a key research priority of the UK PHABSIM user forum 20 years ago (Elliot & Dunbar, 1996), yet never actioned.

Hydrological impacts of climate change are commonly evaluated by using climatic projections, derived from forcing general circulation models with alternative emissions scenarios, to drive hydrological models. Examples of this approach cover hydrological systems at various scales from global assessments (Arnell, 2003; Arnell & Gosling, 2013; Gosling, Bretherton, Haines, & Arnell, 2010; Nohara, Kitoh, Hosaka, & Oki, 2006), through regional (Arnell, 1999) and national scales (Andréasson, Bergström, Carlsson, Graham, & Lindström, 2004), major river basins (Conway, 1996; Nijssen, O'Donnell, Hamlet, & Lettenmaier, 2001; Thompson, Green, Kingston, & Gosling, 2013), medium and small catchments (Chun, Wheater, & Onof, 2009; Thompson, 2012), down to individual sites within catchments (Thompson, Gavin, Refsgaard, Sorenson, & Gowing, 2009). The hydraulic components so often a feature of such models have the potential to be applied to assess the impacts on physical habitat assessment using standard outputs of flow, depth, and velocity. These can enable the calculation of velocity and depth profiles at each time step, and thus represent the flow characteristic throughout an extended simulated period, rather than the few isolated measurements afforded by field surveys. A physical habitat-discharge relationship may thus be produced that is more representative of the range of flows and can incorporate dynamic processes modelled within a river, such as macrophyte growth. This use of hydraulic models in assessing physical habitat availability demands fewer resources, especially within the field, and may be readily applied to rivers through a range of scales and conditions. The idea of using existing hydraulic models for physical habitat assessment has existed for 20 years (Dunbar, 1997a), yet, to our knowledge, never been operationalised. There is a worldwide need to develop approaches for evaluating the impacts of environmental alterations, such as climate change, on fluvial ecosystems.

The aim of this study is to assess the effects of climate change on physical habitat for brown trout (*Salmo trutta*) in a reach of a lowland chalk river. The objectives are to (a) project changes in the inputs to a distributed hydrological or hydraulic model of the river under scenarios of different climate sensitivities to incorporate the uncertainty associated with climate change, (b) use the hydraulic model component to assess how climate change scenarios affect the hydraulic characteristics of the river, and (c) compare simulated hydraulic characteristics under each climate change scenario to the physical habitat requirements of brown trout. In this way, the study provides an assessment of potential ecohydrological impacts of climate change on the river and the subsequent management implications of these impacts.

2 | STUDY AREA

The Centre for Ecology & Hydrology (CEH) River Lambourn Observatory is located in Berkshire, UK (51.445° N, 1.384° W). The site contains a 600 m stretch of the River Lambourn bordered to the west by c. 10 ha of riparian wetland (Figure 1). The catchment area of the Lambourn at the CEH Observatory is approximately 162 km^2. The river drains the Chalk of the Berkshire Downs and is characterised by a large baseflow component. At Shaw, the nearest gauging station 5 km downstream of the observatory, the baseflow index and mean discharge of the Lambourn are 0.96 and 1.73 $m^3\ s^{-1}$, respectively (Marsh & Hannaford, 2008).

The River Lambourn and its associated riparian wetland owe their designation as a site of special scientific interest and special area of conservation to the presence of brook lamprey (*Lampetra planeri*), bullhead (*Cottus gobio*) and Desmoulin's whorl snail (*Vertigo moulinsiana*). The river also holds a designation under the EU habitat directive for water courses of plain to montane levels with *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation.

In addition to brook lamprey and bullhead, there are four species of fish present at the site: brown trout (*S. trutta*), grayling (*Thymallus thymallus*), 10-spinned stickleback (*Pungitius pungitius*), and 3-spinned stickleback (*Gasterosteus aculeatus*). The macrophyte community is dominated by water crowfoot (*Ranunculus* spp. *pseudofluitans* mixed with smaller quantities of *Ranunculus penicillatus* spp. *pseudofluitans* × *Ranunculus peltatus* hybrid). Frequent assemblages of water starwort (*Callitriche* spp.), water parsnip (*Berula erecta*), and watercress (*Rorippa nasturtium-aquaticum*) also occur. Periodic cutting of instream

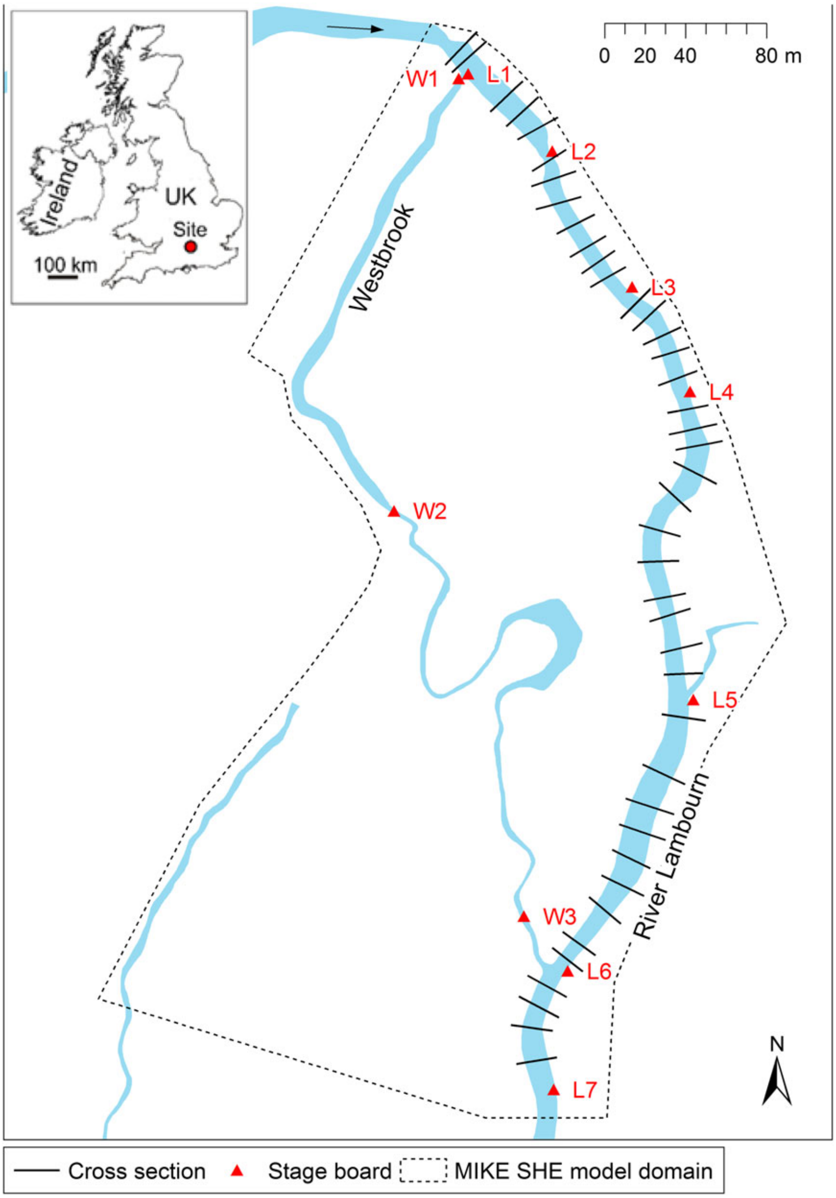

FIGURE 1 The Centre for Ecology & Hydrology River Lambourn observatory, showing the locations of cross sections for the MIKE 11 model and physical habitat assessment, instrumentation network, and MIKE SHE model domain

macrophyte growth is carried out to maintain flood conveyance, lower water levels, and maintain viable fisheries (Old et al., 2014).

Comprehensive hydrological monitoring at the CEH observatory includes observations of wetland groundwater levels from an array of piezometers, described in House, Thompson, Sorensen, Roberts, and Acreman (2015b). Meteorological observations are logged at an automatic weather station installed in the wetland. Observations from seven stage boards are located along the River Lambourn (L1–L7) and three in the Westbrook (W1–W3; Figure 1) are available at an approximately monthly interval. River Lambourn stage is also recorded every 15 min at a stilling well at L2 using a Druck PDCR 1830®. Monthly measurements of discharge are taken at L1 using a Valeport® electromagnetic flow meter.

3 | METHODOLOGY

3.1 | Simulation of baseline conditions

A fully integrated hydrological model of the observatory was developed using the MIKE SHE and MIKE 11 modelling system. The MIKE SHE modelling system simulates the land-based phase of the hydrological cycle (Graham & Butts, 2005), while MIKE 11 provides the one-dimensional (1D) channel component. A detailed description of the full CEH Lambourn Observatory MIKE SHE or MIKE 11 model is provided by House et al. (2015b), whilst this study focusses on the results from the MIKE 11 model.

Channel flow in MIKE 11 is described with the fully dynamic wave formulation of the St. Venant equations, dynamically coupled to MIKE SHE through segmentation of the river into links between adjacent grid squares. Exchanges between MIKE SHE and MIKE 11 occur as bi-directional river-aquifer exchange, overland flow, and flooding. The MIKE SHE model domain was resolved at a grid size of 5 × 5 m, producing 4,261 computational cells. The computational time for each model run was approximately 30 min.

The river network was digitised in MIKE 11 from Ordnance Survey MasterMap 1:1250 raster data. Channel cross-section profiles applied to the network were based on differential GPS (dGPS) surveys conducted at 42 locations along the River Lambourn and 44 along the Westbrook. Bank elevations were extracted from the 5 × 5 m MIKE SHE topographic grid, based on a dGPS ground survey in combination with LiDAR.

Inflows for the upstream channel boundary were specified as a mean 15 min discharge (Figure 2). These were derived from a relationship between the monthly measurements of discharge at L1 (the most upstream stage board; Figure 1) and corresponding flow at the downstream Shaw gauging station. The downstream boundary was set to follow monthly stage observations at L7.

MIKE 11 does not contain a method to explicitly represent volumetric and temporal changes in instream vegetation. To account for macrophyte growth and its removal by cutting within the Lambourn, we adjusted the hydraulic resistance, fundamental to the depth-discharge relationship, as a proxy. Hydraulic resistance was expressed as a 15 min time series of Manning's n coefficients (Figure 2). Values were derived from measurements of cross-section geometry and stage at L1 (Figure 1), energy slope between stage boards at L1 and L2, and the derived 15 min discharge at L1. The time series was applied to the entire reach as a multiplication factor to a fixed channel roughness, with the assumption that variations in macrophyte growth were uniform along the reach. Manning's n values fluctuate between 0.045 and 0.353 in response to the growing season (Figure 2). Increases in discharge from storm events generally correspond to decreases in Manning's n. This is assumed to be due to the flattening or removal of vegetation by the high flows. However, weed cuts within the channel undertaken on 1/5/2013, 16/7/2013, 21/5/2014, and 23/7/2014 caused rapid drops in Manning's n with no equivalent change in discharge.

Calibration of the coupled MIKE SHE and MIKE 11 model was based on groundwater head data from a network of peat and gravel piezometers in the wetland plus comparison between simulated and observed channel stage from 15 min continuous records at L2 and the monthly stage board readings at L1, L3–L7, and W1–W3 (Figure 1). The periods 1/2/2013–1/12/2013 and 1/12/2013–1/10/2014 were used for split sample calibration and validation, respectively. Model performance was based on the Pearson correlation coefficient (R), the Nash-Sutcliffe coefficient (R2, Nash & Sutcliffe, 1970), and the root mean square error of the deviation between observed and simulated groundwater and channel water levels. Performance was classed as "very good" or "excellent" in most cases (Figure S1 and Table S1).

3.2 | Simulation of climate change

This current study employs the same climate change scenarios as House, Thompson, and Acreman (2016). Climate change scenarios were derived for the 2080s using datasets from the Future Flows and Groundwater Levels project (Jackson, Meister, & Prudhomme, 2011; Prudhomme et al., 2012). These include 11-member ensembles of 1 km gridded time series projections (1950–2098) of precipitation, PET (Potential Evapotranspiration), and groundwater levels for Great Britain based on the UKCP09 Hadley Centre's Regional Climate Model HadRM3 run under the medium emissions (SRES A1B) scenario (Murphy et al., 2009). Parameter uncertainty is represented through model variants with different climate sensitivity, which are summarised in Table 1 along with the scenario run id plus the RCM run id and descriptive id used by the Met Office Hadley Centre.

Model inputs of precipitation, PET, groundwater elevation, and river discharge were perturbed for each climate change scenario using a delta factor approach (Thompson, 2012; Wilby & Harris, 2006). Monthly percentage differences between the ensemble reference period (1961–1990) and the future period (2071–2098) were applied to baseline values over the full simulation period 1/2/2013–1/10/2014. Monthly delta factors for precipitation (%), PET (%), and groundwater level (m) were extracted from the relevant 1 km grid square of the

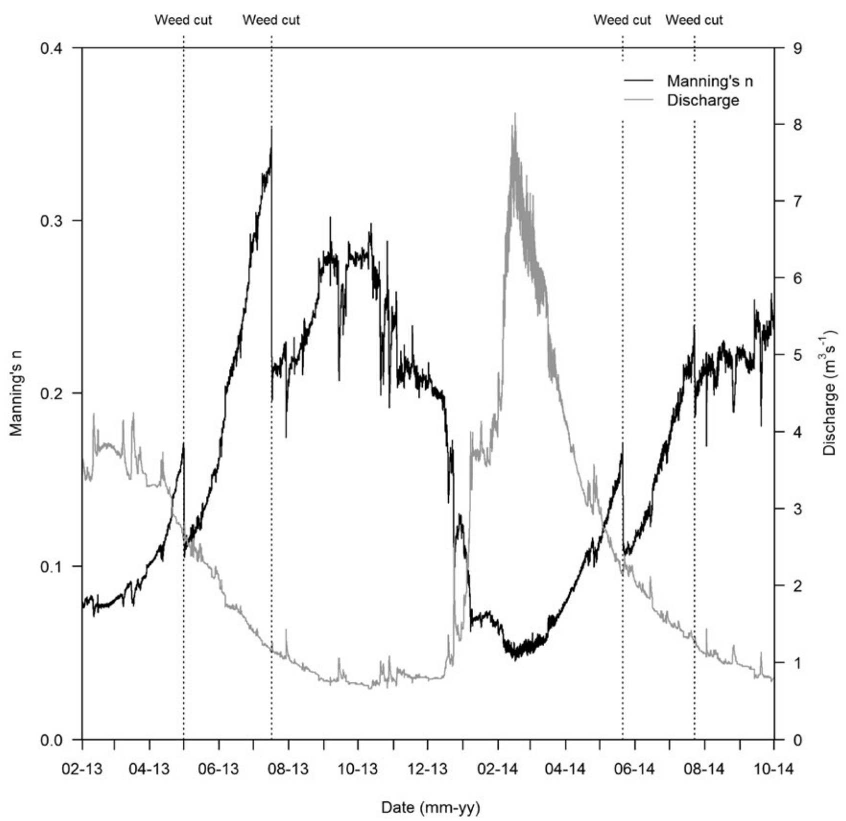

FIGURE 2 Calculated Manning's n roughness coefficient and discharge inputs for the MIKE 11 hydraulic model for the river Lambourn

TABLE 1 Climate sensitivities, run ID, and model variant name for the HadRM3-PPE ensemble of climate projections (after HCCPR, 2008)

Run ID	Climate sensitivity	RCM run ID	RCM name
A	3.53485	Afgcx	HadRM3Q0
B	2.58475	Afixa	HadRM3Q3
C	2.81543	Afixc	HadRM3Q4
D	3.43839	Afixh	HadRM3Q6
E	4.39594	Afixi	HadRM3Q9
F	3.89523	Afixj	HadRM3Q8
G	4.44284	Afixk	HadRM3Qk
H	4.88248	Afixl	HadRM3Q14
I	4.54486	Afixm	HadRM3Q11
J	4.79648	Afixo	HadRM3Q13
K	7.11014	Afixq	HadRM3Q16

future flows dataset. Climate change delta factors for discharge were not available from future flows and were instead obtained through development of a lumped rainfall-runoff model of the Lambourn catchment at Shaw using MIKE NAM (DHI, 2009). Following model calibration, climate change delta factors for discharge were derived by running the NAM model with catchment averaged precipitation and PET under each of the 11 HadRM3 ensemble members. These factors, expressed as a percentage, were subsequently applied to the original stream inflows used within the MIKE SHE model.

3.3 | Physical habitat modelling

To assess physical habitat, we converted depth and velocity characteristics of the River Lambourn to habitat availability metrics using habitat suitability indices (HSI) following the PHABSIM methodology (Bovee, 1982; Waddle, 2001). HSI for juvenile (0–7 cm) and adult (8–20 cm) brown trout (*S. trutta*) based on velocity and water depth were taken from Dunbar et al. (2001; Figure 3). Bed substrate was not included as a parameter as the river has a uniform gravel bed. The River Lambourn channel morphology was derived from a total of 41 cross sections with an average spacing of 14.9 m, providing a total bed area 6735.1 m^2 and reach length 609 m (Figure 1). The distances between cross sections provided the longitudinal lengths for a multi-dimensional matrix of cells with different bed areas and volumes, and, thus, hydraulic parameters. Transverse lengths were derived from changes in bed elevation from cross-section points, resulting in 641 computational cells. Water depths for each cell were calculated from hydraulic model outputs of channel stage. The 1D velocity outputs were disaggregated to each cell by the ratio of cell flow area to total flow area for the cross section. Depth and velocity for each cell were evaluated against the HSI and combined over the full range of discharges for the baseline, individual scenarios, and scenario mean. These were totalled for the reach to produce available physical habitat, expressed as weighted usable area (WUA) in m^2 1000 m^{-1} of river (Equation 1), as a function of discharge for the baseline:

$$\mathrm{WUA} = \frac{\sum_{i=1}^{n} a_i v_i d_i}{l}, \tag{1}$$

where a_i is the surface area of cell i, v_i is the suitability associated with velocity for cell i, d_i is the suitability associated with depth in cell i, and l is the reach length in 1000 m (0.609). The slope of the output curve describes the physical habitat sensitivity to flow. WUA was also expressed as a time series for the baseline, individual scenarios, and the scenario mean.

To validate the model against observations, we took hydraulic measurements from a field survey conducted between March and June 2015. Three distinct periods were identified to coincide with particular flow and vegetation conditions: (a) winter high flows outside of the growing season, with minimal vegetation (10/3/2015–31/3/2015), (b) summer low flows before the weed cut with abundant vegetation (7/5/2015–12/5/2015), and (c) summer low flows after the weed cut with reduced vegetation (29/5/2015–8/6/2015). The weed cut took place on 13/5/2015. Velocity profiles and stage measurements were taken at each period for a total of 14 cross sections (Figure S2). Velocity was measured using a Valeport Ltd. Model 802 electromagnetic flow meter. The study reach comprised a total bed area 4956.4 m^2 and length 488.3 m, reducing to 4514.1 m^2 and 442.6 m in period 2 because of high waters restricting accessibility. The same HSI for juvenile trout as that used in the modelling study was applied

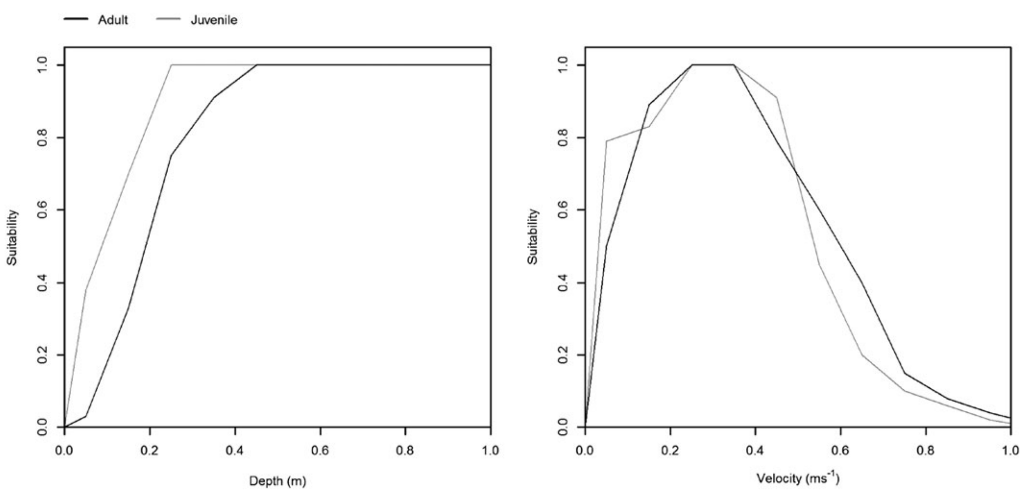

FIGURE 3 Habitat suitability indices for brown trout (*Salmo trutta*; after Dunbar et al., 2001)

TABLE 2 Flow duration summary for the river Lambourn baseline simulated period (1/2/2013–1/10/2014)

Percentile	Discharge (m^3 s^{-1})
Q_2	6.81
Q_5	5.96
Q_{10}	4.15
Q_{25}	3.39
Q_{50}	1.69
Q_{75}	0.95
Q_{90}	0.79
Q_{95}	0.75
Q_{98}	0.72
Q_{mean} = $Q_{40.5}$	2.29

to derive total WUA for the measured discharge. Results were standardised to percentage area cover for comparison with results from the 1D model based upon similar discharge and conditions.

4 | RESULTS

4.1 | Baseline flow and physical habitat characteristics

The low gradient flow duration curve and percentage exceedance flows indicate a non-flashy regime (Table 2 and Figure 4a). Mean discharge for the baseline simulation period was 2.29 m^3 s^{-1} corresponding to 39.9% exceedance, whilst the magnitude of the flow exceeded 50% of the time was 1.69 m^3 s^{-1}. The influence of the regime on stage, velocity, and, thus, available physical habitat is unclear, as there is no well-defined curvilinear relationship (Figure 4b-d), although the relationship between velocity and discharge does show a clear positive trend. The distribution of available physical habitat against discharge bears greater similarity to stage than velocity, although it is not a precise match. Overall, several values of stage, velocity, and physical habitat exist for distinct discharges. This is most apparent below the 10% exceedance flow of 4.15 m^3 s^{-1}, above which the flow duration curve steepens noticeably, and the point distributions for physical habitat, stage, and velocity against discharge converge to closer relationships.

The amount of available habitat appears greater for juvenile than adult brown trout at flows below 3.5 m^3 s^{-1}. More habitats are available for adult trout when flows are between 3.5 and 5.0 m^3 s^{-1}, whilst at discharges above 5.0 m^3 s^{-1} habitat availability for juveniles and adults is similar (Figure 4d). Adult trout exhibits a greater range of habitat availability than juvenile trout from the WUA for the flows simulated. There is a greater difference between the minima than maxima for each life stage. Availability of baseline physical habitat varies considerably over the simulation period (Figure 5). Conspicuous peaks on and around 28/4/2013, 22/6/2013, 20/5/2014, and 20/7/2014 occur shortly before dramatic reductions caused by the weed cuts. The largest of these sudden drops on 1/5/2013 represents a decrease in available habitat by 1690 m^2 1000 m^{-1} (15.3%) for adult and 1790 m^2

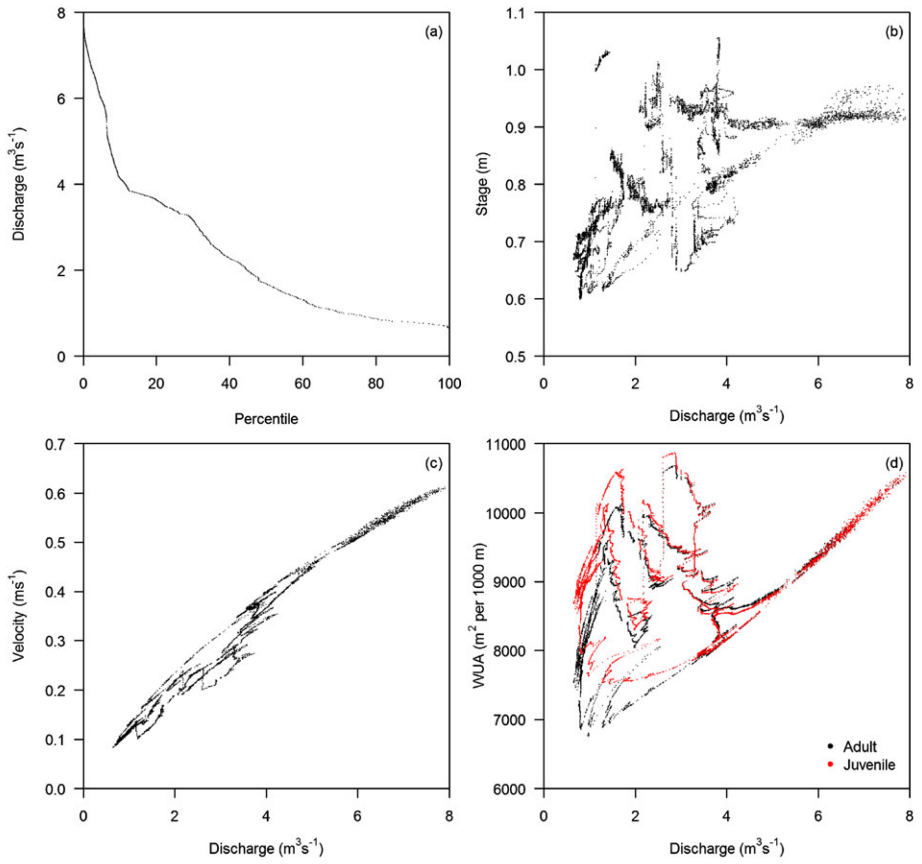

FIGURE 4 Simulated relationships between (a) flow and physical habitat availability, (b) flow and percentage exceedance, (c) flow and stage, and (d) flow and velocity for the river Lambourn

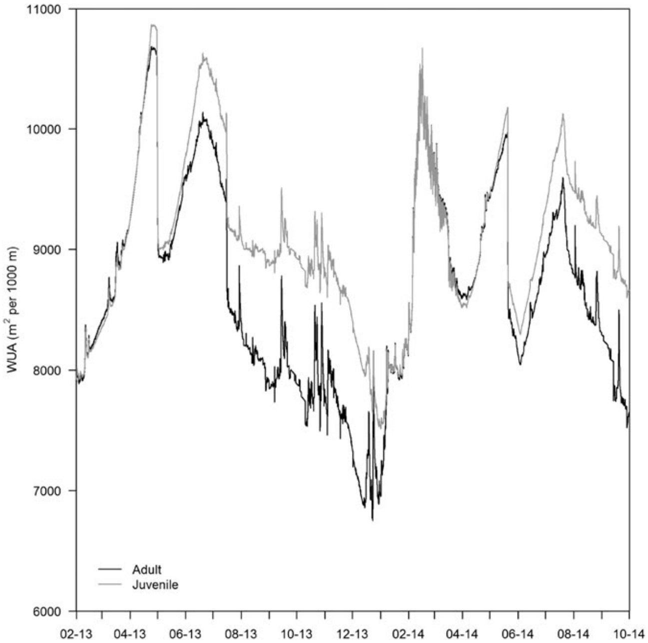

FIGURE 5 Simulated baseline physical habitat availability for adult (8–20 cm) and juvenile (0–7 cm) brown trout (*Salmo trutta*) and validation values from field survey periods for the river Lambourn: (1) winter high flows outside of the growing season, with minimal vegetation (10/3/2015–31/3/2015), (2) summer low flows pre-weed cut with abundant vegetation (7/5/2015–12/5/2015), and (3) summer low flows post-weed cut with reduced vegetation (29/5/2015–8/6/2015)

1000 m^{-1} (16.2%) for juvenile trout. A prolonged period of declining habitat extends from the weed cut on 22/6/2013 to 23/12/2013 and is associated with persistent low flows and relatively high Manning's n (Figure 2). This precedes the largest sustained increase in habitat, which culminates in the peak on 15/2/2014, and corresponds to a period of high flow. Values of habitat availability and discharge during and immediately after this high flow period display much higher daily variability compared to any other time. Elevated available habitat match periods of high stage (see Figure A1).

Habitat availability for adult trout generally falls below that for juveniles. This difference is as much as 1148.5 m^2 1000 m^{-1} (10.4%, 11/10/2013) during periods of low flow (e.g., July 2013 to February 2014 and August 2014 to October 2014). Contrasting periods of high flow display greater similarity in habitat availability of juvenile and adult trout, and they are equivalent through April 2013 and January to March 2014. Available physical habitat is greater for adult trout in two periods, February 2013 to April 2013 and March 2014, although the differences are relatively small.

Comparison of values of WUA for juvenile trout from the field survey (Table 3) and modelled values indicates good agreement. For period 1, outside of the growing season and with a discharge of 1.77 m^3 s^{-1}, the surveyed WUA was 69.2% of the area while the corresponding modelled WUA was 68.0% (1/1/2014). Period 2 (discharge of 1.26 m^3 s^{-1} prior to a weed cut in the growing season), resulted in 81.1% of the area available as habitat for juvenile trout compared to 86.9% modelled (8/7/2014). Period 3 (discharge of 1.34 m^3 s^{-1} after a weed cut), resulted in 78.9% available habitat from the field survey and 82.4% from the model (2/8/2013). The model tends to over predict available habitat for similar discharges within the growing season, and to under predict the value outside of the growing season. However, differences, between 1.2% and 5.8%, are very small.

4.2 | Climate change impacts on hydraulic characteristics

As reported in House et al. (2016), monthly delta factors for the scenario mean indicate a decrease in discharge from baseline values throughout the year (Figure 6a). Declines are largest in October and lowest in March. Only four individual scenarios project increased discharge at any time of the year, while the remaining eight show declines in discharge throughout the year. Application of change factors to the baseline discharge data results in a decrease in mean discharge for all but two of the scenarios (C and D; Figure 6b). For the scenario mean, the mean discharge declines by 0.19 m^3 s^{-1} (Table 4).

A general reduction in both stage and velocity is indicated by climate change projections, which is more apparent during periods of low flow in July 2013–December 2013 and August 2014–October 2014 (Figures S3 and S4). Scenario mean projections show that the largest decreases are in December 2013. Stage drops to near zero at L1, L3, L4, and W3 in December 2013, while at no point does the scenario mean show increases in velocity. At high flow periods, values for both stage and velocity correspond very more closely to baseline values, particularly in March 2013. Inter-scenario variations in stage are more pronounced than for velocity.

For the 11 scenarios, changes in mean simulated stage appear similar at all locations, with the exception of W2 (Figure S3). Averaged changes in simulated stage show that the Westbrook have a slightly exaggerated response compared to the Lambourn (Table 4), although this is likely due to the influence of the results for W2. At W2, stages generally fall below baseline levels, except during periods of high flow, while the December minimum is not as apparent as it is at other locations.

Velocities in all scenarios for the simulation period rarely exceed 1 ms^{-1}. Locations with relatively high initial velocity (L1, L3, L4, L5, and L6) show greater variation in velocity through the simulation period than those with lower initial velocity (L2, L7, W1, W2, and W3). This is especially apparent when comparing the rapid changes in velocity at times of weed cuts, which range from a 0.182 ms^{-1} rise under baseline conditions on 1/5/2013 at L5 to almost no

TABLE 3 Validation conditions and physical habitat availability from the river Lambourn field survey (March–June 2015)

Period	Dates	Growing season	Pre/post weed cut	Discharge (m^3 s^{-1})	WUA (m^2 per 1000 m)	Bed area (m^2)	Percentage cover (%)
1	10/3/2015–31/3/2015	N	N/A	1.77	7020.1	4956.4	69.2
2	7/5/2015–12/5/2015	Y	Pre	1.26	8273.7	4514.1	81.1
3	29/5/2015–8/6/2015	Y	Post	1.34	8005.8	4956.4	79.1

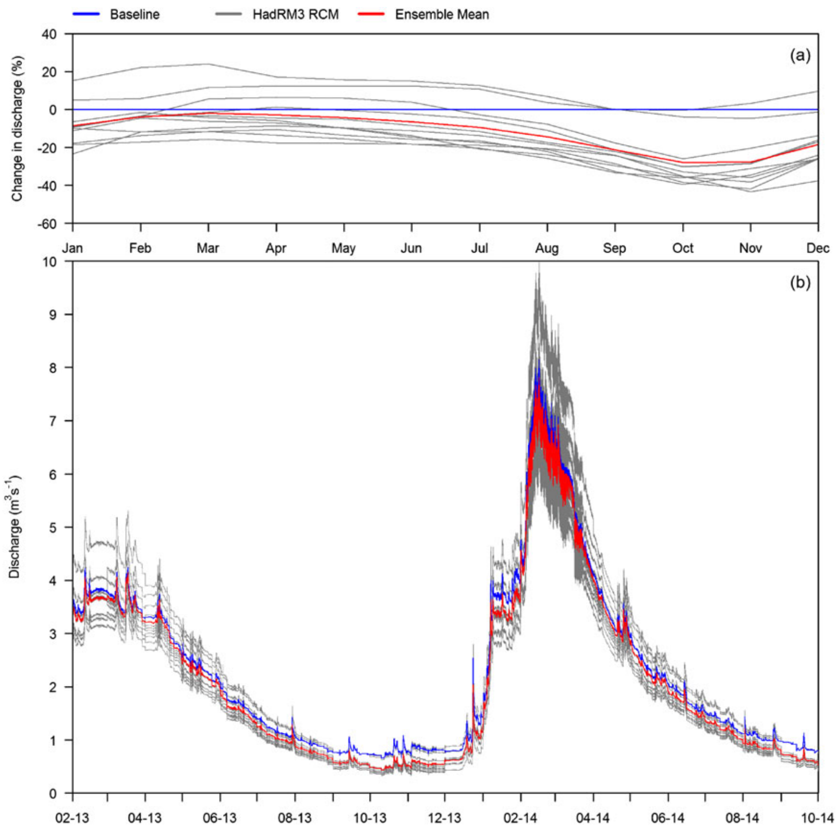

FIGURE 6 Projected climatic changes in river Lambourn discharge for the 2080s by individual scenario and scenario mean: (a) monthly percentage change and (b) applied absolute change

TABLE 4 Baseline mean river Lambourn discharge ($m^3\ s^{-1}$), simulated baseline mean river Lambourn and Westbrook channel stage (m), and velocity (ms^{-1}), river Lambourn physical habitat availability (WUA, $m^2\ 1000\ m^{-1}$) for adult (8–20 cm) and juvenile (0–7 cm) brown trout (*Salmo trutta*) and changes for climate change scenarios and mean for the full simulation (1/2/2013–1/10/2014) period. Italicised values indicate negative changes

		Stage		Velocity		WUA	
Run ID	Discharge	Lambourn	Westbrook	Lambourn	Westbrook	Adult	Juvenile
Baseline	2.37	0.44	0.47	0.360	0.159	8639.8	9071.8
A	−0.16	−0.02	−0.03	−0.012	−0.006	−308.0	−204.7
B	−0.44	−0.06	−0.08	−0.033	−0.021	−681.3	−468.8
C	0.19	0.02	0.03	0.012	0.008	141.8	116.4
D	0.42	0.04	0.05	0.023	0.016	308.8	260.0
E	−0.06	−0.01	−0.01	−0.005	−0.002	−186.6	−116.2
F	−0.31	−0.05	−0.06	−0.024	−0.014	−583.1	−392.4
G	−0.27	−0.05	−0.06	−0.022	−0.013	−558.5	−372.0
H	−0.39	−0.05	−0.07	−0.029	−0.018	−634.6	−436.8
I	−0.48	−0.06	−0.08	−0.034	−0.022	−640.2	−445.5
J	−0.21	−0.03	−0.04	−0.016	−0.009	−386.2	−258.3
K	−0.40	−0.05	−0.06	−0.028	−0.018	−596.2	−410.7
Mean	−0.19	−0.03	−0.04	−0.014	−0.008	−349.4	−232.9

discernible change in the Westbrook locations. Averaged changes show an exaggerated response in the Lambourn compared to the Westbrook (Table 4).

4.3 | Climate change impacts on physical habitat availability

The impacts of the climate change scenarios on physical habitat availability are greater for adult rather than juvenile trout, especially during periods of low flow between July 2013–December 2013 and August 2014–October 2014 (Figure 7). Velocities are generally within the optimal or near optimal HSI range for brown trout, falling outside during periods of extreme low or high flow. Stage values largely fluctuate through optimal and suboptimal HSI ranges.

Impacts are highlighted by the scenario mean decrease averaged over the simulation period (Table 4). At no point over the full simulation period does the scenario mean shows an increase in habitat availability for either life stage (Figure 7). The largest mean decreases occur

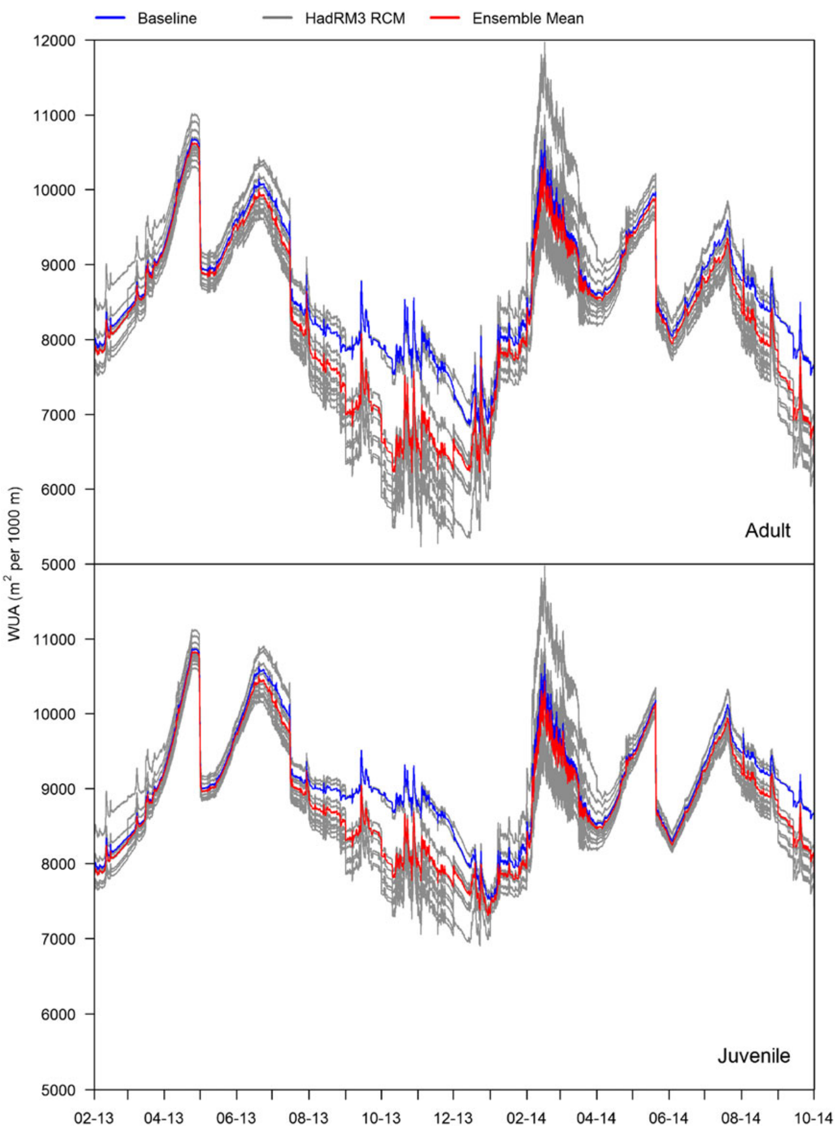

FIGURE 7 Simulated baseline, projected scenarios, and mean physical habitat availability for adult (8–20 cm) and juvenile (0–7 cm) brown trout (*Salmo trutta*) in the river Lambourn

in October 2013, whilst closest correspondence with baseline values is seen in March 2013.

Of the individual scenarios, four (A, C, D, and E) project increases in available habitat from baseline values on at least 1 day. For scenario A, this is only in April 2013 and 2014. In contrast, results for scenario D only drop below baseline values in October and then by relatively little. The greatest increases are projected by scenario D on 15/2/2014, with the largest inter-scenario range also occurring at this time. Of the other scenarios, which all display reductions in physical habitat, the greatest single decrease is for scenario K on 3/11/2013. The smallest inter-scenario range occurs in mid May 2013 for adult trout, and the beginning of June 2014 for juvenile trout.

5 | DISCUSSION

Output time series from a MIKE 11 1D hydraulic model of the River Lambourn have allowed the effects of macrophyte growth and its management to be incorporated into an assessment of climate change impacts on physical habitat availability. The effects of management (weed cutting) are just as noticeable as those of climate change, with overall reductions in habitat availability and consequent implications for the aquatic ecology. Although this has been demonstrated for only a single species, brown trout, the method may be applied to other species for which HSIs are available, including other salmonids (Dunbar et al., 2001) and macroinvertebrates (Gore et al., 1998). Rather than using a single rating curve, the area of available physical habitat has been calculated at each time step over the full simulation period for baseline conditions along with each climate change scenario and the scenario mean. This challenges the assumption, contained within physical habitat modelling approaches such as PHABSIM, that relationships between discharge and hydraulic characteristics are time invariant. The more flexible approach presented here is more in line with common hydrological and hydraulic assessments of climate change (e.g., Chun et al., 2009; Thompson, 2012; Thompson et al., 2009), and opens the way for similar use of models that are able to represent dynamic systems.

The availability of habitat for adult brown trout is found to be more susceptible to low flows than that for juvenile trout. Although brown trout exhibit a habitat generalist strategy, with flexibility in preference across life stages, the spatial scale and pattern of hydraulic variables are important for habitat selection (Ayllón, Almodóvar, Nicola, & Elvira, 2010; Heggenes, 2002). Adult brown trout often depends on deep water for shelter, whilst fry may flourish in shallow riffle habitats (Armstrong & Nislow, 2012; Nislow, Einum, & Folt, 2004). Here, stage appears to be the dominant factor in controlling the baseline amount of available habitat, expressed in the similarity of the stage-discharge relationship to the physical habitat-discharge relationship (Figure 4). Relatively, low velocities are indicative of the position of the reach in a lowland catchment with a relatively slow runoff response and large baseflow component (Marsh & Hannaford, 2008). With weed cuts occur coincident sharp and relatively large reductions in stage and, thus, habitat availability. These introduce a degree of stress that may impact adult brown trout more than juvenile life stages.

Periods of low flow are also associated with an amplified response of available physical habitat to climate change in most scenarios. Whereas, at high flows, differences in habitat availability between the two life stages become less apparent. Results further indicate that climate induced changes in habitat availability for brown trout will be depth limited by the hydraulic geometry. Decreases in water depth at low flows may reduce the accessibility to preferred habitat for feeding and increase fish density, particularly if unable to redistribute (Armstrong & Griffiths, 2001). At higher densities, there is a greater risk of hypoxia and predation, which may include cannibalism (Smith & Reay, 1991). Temperature increases through low flow periods occurring through the summer months, June to August, could exaggerate the negative impacts of low flows. During drought conditions, increased temperature in pools has been linked to increased mortality for salmonids (Elliott, 2000), and will exacerbate hypoxia (Milner et al., 2003). During winter, low flows may increase the risk of freezing and mortality rates (Huusko et al., 2007). However, as a chalk stream fed predominantly by groundwater, the River Lambourn is thermally stable all year round (House et al., 2015a). Seasonal temperature fluctuations are minimal and unlikely to be significant against the loss in habitat. Thus, deeper sections of the river in which velocity is more stable, such as pools, may provide refuge areas for brown trout during periods of stress induced by reduced flow. Stretches with relatively low stage and higher, more variable velocities (L1, L3–5), most likely representing fast runs, are likely to be impacted the most by climate change.

Although an overall reduction in habitat availability is projected, the responses reflect some uncertainty in the hydrometeorological drivers for discharge inputs to the MIKE 11 model. Inter-scenario member variations differ over time and exhibit seasonality in the nature of these changes. An existing vulnerability of brown trout during low summer flow periods is exaggerated in projections from nine of the 11 scenarios, especially for the adult life stage. These nine members project general reductions in habitat availability through the full simulation period. In the other two scenarios (C and D), there is an overall increase in habitat availability in all periods although it is close to baseline values during periods of low flow. Nevertheless, without modifications to current management practices, the available physical habitat for brown trout would decline under the majority of climate change scenarios.

Periods of high flow and abundant macrophyte coverage are associated with large areas of available physical habitat; while at low flows following weed cuts, the habitat availability is at its lowest. Management of macrophytes through weed cutting is generally undertaken to achieve various target functions (Baattrup-Pedersen & Riis, 2004), including flood water conveyance (Baattrup-Pedersen, Skriver, & Wiberg-Larsen, 2000), water level control, and viable fisheries (Old et al., 2014). Submerged plants within watercourses, aside from their hydraulic significance, are generally seen as beneficial for fish because of the provision of habitat for invertebrate prey, shelter and protection, and oxygen production (Bursche, 1971; Garner, Bass, & Collett, 1996). Fish distribution in uncut and partially cut channels has been shown to be strongly associated with weed cover (Swales, 1982), whilst macrophyte growth has been advocated for maintenance of habitat (Hearne & Armitage, 1993). Without weed cuts, it is debatable whether flow responses to climate change would have had as large effects on habitat availability.

In the River Lambourn, weed cuts are primarily for flood risk reduction (Old et al., 2014), as the reduced flow resistance and volume decrease from vegetation removal increases the conveyance capacity of the river and reduces stage. This has important social and economic implications for the surrounding community, which previous events (e.g., Morris & Brewin, 2014; Pitt, 2008) have shown to be politically charged. There is the potential to rethink the management regime for macrophytes in order to reduce the negative environmental effects whilst maintaining flood resilience and at the same time mitigating the impacts of climate change. Other studies have posited spatially varied configurations for weed cutting (Baattrup-Pedersen & Riis, 2004; Garner et al., 1996), and regulating the timing of cuts in relation to plant growth (Westlake & Dawson, 1982) to limit impacts on macrophyte diversity and fish habitat. The MIKE SHE and MIKE 11 and physical habitat modelling system employed in this study could be used to this effect through the simulation of alternative weed cutting strategies encompassing different degrees of removal, spatially varying cuts, and alternative timings. The use of hydraulic models in this way to assess the impacts of environmental change upon physical habitat has enormous potential for application to rivers where stage-discharge relationships are unclear due to factors including seasonal macrophyte growth.

Validation values for available physical habitat, although close to those modelled, are indicative only. The field survey was undertaken the year after the simulation period, and encompasses a section of the reach with a different area and fewer cross sections. An extension of the model simulation period to incorporate the field survey period was not possible because of availability constraints on meteorological and groundwater level data. Nevertheless, both sets of results exhibit the rise and fall in habitat availability due to the macrophyte growth season and its management. When compared at times with similar conditions and identical flows, the values are reassuringly close.

Discretised spatial differences in vegetation are not included in this study. Assumption of a universal Manning's n value over the reach, plus disaggregation of velocity profiles across cross sections, does not allow for local small-scale variations (microhabitat) and renders such a spatial evaluation inappropriate. An assessment of this order would require a field survey before and after a defined change in conditions, such as a weed cut. On the reach scale, however, where these variations average out, and validation to stage is excellent, the method provides a useful means of assessing the impacts of climate change.

6 | CONCLUSION

Assessment of physical habitat availability for brown trout over the model simulation period revealed the projected impacts of an ensemble of climate change scenarios. An overall reduction in habitat availability was larger for adult rather than juvenile brown trout. Impacts were most pronounced during summer months, accentuating periods of low flows and reduced habitat. Model results also highlighted the impact of weed cutting on flow depth, velocity, and, adversely, on habitat availability. However, adjustments to the management regime have potential for simultaneously mitigating both flood risk and the ecological impacts of climate change.

The influence of macrophyte growth and its management on stage and velocity caused the physical habitat-discharge relationship itself to be unusable in evaluating the sensitivity of brown trout to changes in flow. As macrophytes are a feature of many lowland river systems, this raises concerns over the suitability of standard physical habitat modelling methods to regulatory and research applications. Indeed, any process that causes different velocities and depths for a particular flow renders the physical habitat-discharge relationship potentially irrelevant. Such processes, which also include sediment transport and deposition, groundwater or overbank exchange, ice cover, morphological change, and river management practices, are common features of fluvial systems and are integral to the unique character of many rivers. This shortcoming could be overlooked in a field survey, where profile measurements are taken for a few specific flow rates. Application of the MIKE 11 hydraulic component of the MIKE SHE model has elucidated the variability in flow conditions and, thus, habitat availability for a macrophyte dominated river.

Although results from a distinct field survey in the same reach are supportive of modelled values of physical habitat availability, the study would benefit from further validation. In addition, direct effects of climate change on instream vegetation through increases in temperature and carbon dioxide have not been accounted for. The disaggregation approach of one-dimensional values to profiles across cross sections does not allow for local variations and spatial analysis. However, it is considered robust when projecting impacts for the reach as a whole. The effect of weed growth on the vertical velocity profile is not accounted for, as it would require resource intensive 3D hydraulic modelling, which is beyond the scope of this study. The use of outputs from hydraulic models in assessing impacts of environmental change on physical habitat availability is cost-effective, efficient, and has international applicability.

ACKNOWLEDGMENTS

Thanks to Ponnambalam Rameshwaran at CEH for River Lambourn discharge measurements. Data for future flows and groundwater levels and GEAR (Gridded Estimates of Areal Rainfall) were obtained from the CEH Environmental Information Platform (https://eip.ceh.ac.uk/). PET data were derived from UK Met Office MORECS. The Environment Agency Geomatics Group provided LiDAR data. Ordnance Survey MasterMap data are ©Crown Copyright and an Ordnance Survey/EDINA supplied service. Thanks are extended to all other data providers and field support. Funding for the study was provided by the Natural Environment Research Council (NERC; ref. NE/K500951/1).

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SUPPORTING INFORMATION

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How to cite this article: House AR, Thompson JR, Roberts C, de Smeth K, Old G, Acreman MC. Projecting impacts of climate change on habitat availability in a macrophyte dominated Chalk River. *Ecohydrology*. 2017;10:e1823. https://doi.org/10.1002/eco.1823