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Catchment-scale applications of hydraulic habitat models: Climate change effects on fish

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Abstract

Approaches available for estimating the ecological impacts of climate change on aquatic communities in river networks range from detailed mechanistic models applicable locally to correlative approaches applicable globally. Among them, hydraulic habitat models (HABMs) link hydraulic models of streams with biological models that reflect how organisms select microhabitat hydraulics. Coarser but more general species distribution models (SDMs) predict changes in geographic distributions; they generally involve coarse predictors such as air temperature or distance to source but neglect proximate habitat descriptors such as microhabitat hydraulics. We propose an original application of HABM for predicting the ecological impacts of climate change at large scales, a comparison of their predictions with those of SDM and a linkage of the two modelling approaches. We showcase our approach in a large catchment (Rhône River) where an available distributed hydrological model estimates present and future unregulated daily flows over the whole river network. Despite large local uncertainties, simulations showed that climate change may strongly reduce low flow percentiles (e.g., a median reduction of 38.6% for a pessimistic climate scenario), inducing important alteration of fish hydraulic habitat suitability (e.g., a median loss of 3.9%–18.7% for three modelled fish species with contrasting habitat use: brown trout, barbel and sculpin). The HABM and SDM individually predicted consistent or opposite fish responses to climate change, depending on the species and their habitat requirements. Our results illustrate that accounting for ecological responses to proximate habitat variables such as hydraulics can strongly modify projections related to climate change.

KEYWORDS
catchment management, climate change, ecohydraulics, fish habitat, hydraulic geometry model, hydrological model, species distribution model

1 | INTRODUCTION

Global and climatic changes will strongly alter thermal regimes in river networks and the occurrence of extreme hydrological events (Stahl et al., 2010; Vidal et al., 2016), including low flows. Knowledge of the ecological consequences of these changes and their spatial distribution in river networks is needed to find improved compromises between water uses and ecological status. This is particularly true in large, diverse river catchments, where water uses are varied and their spatial distribution complex.

Many approaches aim at predicting the impacts of climate change on aquatic communities in river networks. Approaches range from

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coarse ecological models applicable globally to detailed, mechanistic ecological models generally applied locally. For example, models based on 'species–discharge' relationships (i.e., correlations between species richness in catchments and discharge at their mouths) have been used to predict fish species loss globally (Iwasaki et al., 2012; Xenopoulos & Lodge, 2006). Predictions by these large-scale correlative approaches can be influenced by non-causal correlations that make them unrealistic (Damiani et al., 2019; Tedesco et al., 2013). In particular, intercorrelations between catchment discharge, total and wetted areas and temperature may influence large-scale predictions. At the other end of the spectrum, models of populations dynamics taking into account the effects of proximate habitat variables such as reach hydraulics or water temperature may well reflect observed annual changes in fish abundance (Bret et al., 2017) and provide predictions of the effects of climate change (Ayllón et al., 2019). Such detailed, more mechanistic models contribute to identifying effective local management measures. However, they may have limited transferability and use input variables and calibration data that are not available at large scales.

Species distribution models (SDMs) predict species occurrence in river reaches from reach- and catchment-scale descriptors. They have been widely used to understand and predict the effects of climate change on species spatial distribution at the scale of large catchments (Buisson & Grenouillet, 2009; Radinger et al., 2017). They have an intermediate position in the spectrum described above, because they take into account many reach-scale environmental factors that may influence species geographic distributions. These factors often include air temperature, a wide range of topographic and climatic data (e.g., slopes, catchment area, catchment use and rainfall) and optionally coarse hydrologic or geomorphic information (e.g., hydro- or ecoregions). Therefore, SDM calibration with field data helps understand the relative role of environmental predictors on the observed spatial distribution of species. Although mostly calibrated in space, SDMs have been used to predict temporal changes in species distributions. For example, Comte and Grenouillet (2015) used SDM to show that the observed distributional shifts of fish species towards higher altitudes with climate warming were slower than expected according to isotherm shifts. Yet, the transferability of SDM across several catchments remains little tested, and few SDMs involve key proximate habitat descriptors such as water temperature or microhabitat hydraulics (Gies et al., 2015; Huang & Frimpong, 2016; McGarvey et al., 2018). Due to their calibration in space and over large areas, SDMs generally well reflect the effect of wide climatic gradients and have been mostly used for predicting the effects of warming rather than those of hydrological changes.

Hydraulic habitat models (HABMs) link hydraulic models of stream reaches with biological models of hydraulic microhabitat selection by organisms (Tharme, 2003) to predict hydraulic habitat suitabilities for different fish species. Within the spectrum of approaches, they are closer to local mechanistic approaches than SDMs (Lamouroux et al., 2017). HABMs are widely used in the context of 'environmental flow' definitions, for predicting the impacts of temporal hydrological changes (e.g., due to water abstraction or diversion) on the physical habitat of aquatic organisms at a given location (Dunbar et al., 2012). They differ from SDMs in several ways. First, they focus on marginal responses to hydraulic changes (current velocities and water depths) under low to medium discharge rates. Second, they are based on patterns of habitat selection observed at the microhabitat scale (e.g., a few square metres for fish), within stream reaches, for separating hydraulic effects from others. Third, they are expected to predict temporal changes in species abundance rather than species spatial distribution. HABMs have proved useful for predicting the observed effects of water abstraction on species relative abundance (Lamouroux et al., 2014). However, they focus on the effects of physical alterations only and have been mostly applied to local environmental flow studies with available descriptions of hydraulics in stream reaches.

Bridging gaps between local mechanistic models and global ones, by refining global models or upscaling local ones, has been a long-lasting objective of ecologists (Peckarsky et al., 1997). Upscaling HABMs at catchment to global scales is particularly attractive for predicting the ecological consequences of hydrological alterations while taking into account the effects of microhabitat hydraulics. Early upscaling attempts of HABMs required important simplifications for describing microhabitat hydraulics at large scales (Singh & McConkey, 1989). Three important elements suggest that improved large-scale applications are now achievable. First, improved descriptions of reach-scale hydraulics at large scales are available, based on the analysis of intercontinental hydraulic geometry (HG) data (Morel et al., 2020). Second, hydraulic habitat suitability for different species can be predicted from reach-scale hydraulics using simplified, statistical HABMs (Lamouroux & Capra, 2002). Third, biological models of microhabitat selection by aquatic taxa have shown a high degree of generality among rivers and seasons (Lamouroux et al., 2013, for macroinvertebrates; Plichard et al., 2020, for fish). These progresses enable to predict the sensitivity of aquatic habitats to water abstraction in large catchments (Damiani et al., 2019; Miguel et al., 2016; Snelder, Booker, & Lamouroux, 2011) or globally (Damiani et al., 2021). This suggests that upscaling HABMs for predicting the ecological consequences of climate change in large catchments is now possible.

The primary objective of this methodological study is to describe an original application of HABMs in a large catchment for predicting the effects of climate change on hydraulic habitat suitabilities. For this purpose, we link a HABM (for three illustrative fish specific life stages) with a distributed hydrological model that predicts discharge rates, a model of stream reach HG that translates discharge into hydraulics and an SDM that predicts species geographic distributions. We showcase our methods with simulations in the Rhône catchment in France comparing a present period (1987 to 2012) and a future period (2075 to 2100), based on two alternative climatic scenarios and partly accounting for model uncertainties.

Although the SDM development is not the main focus of this modelling exercise, a secondary objective is to compare projections of species spatial distributions provided by the SDM and changes in hydraulic habitat suitabilities provided by the HABM. Based on this comparison, we discuss how the different hydrological and ecological models involved can complement themselves for an improved prediction of the ecological impacts of climate change.

2 | MATERIAL AND METHODS

2.1 | Study area

We applied our approach to the French part of the Rhône River basin, of approximately 86,000 km^2, due to the availability of a distributed hydrological model covering the catchment (Figure 1). The Rhône catchment has a very heterogeneous climate (mean annual rainfall between 620 and 2190 mm per year and mean air temperature between −1.5 and 14.7°C) and geology (Figure 1). River flow regimes range from glacial or nival in the Alps (with low flows in winter and higher flows in spring) to the Mediterranean (with dry summers and strong rainfall events in other seasons) (Sauquet et al., 2008). For example, the three sub-catchments shown in Figure 1, corresponding to a subdivision used by water managers, are dominated by different regimes: The Upper Isère sub-catchment is mostly influenced by snowmelt, the Doubs is mostly pluvial and the Durance sub-catchment combines snowmelt influences in the mountains and Mediterranean influences downstream.

2.2 | Modelling framework

Our global approach (Figure 2) was to link a distributed hydrological model, a model of stream reach hydraulics (HG model), an SDM and a HABM to predict possible effects of climate change on fish distribution and habitats.

For simulations, we used a digital-oriented theoretical hydrographic network (Réseau Hydrographique Théorique [RHT]; Pella et al., 2012) comprising around 115,000 reaches across France among which 18,226 are in the Rhône catchment. We chose this network rather than others available at the European scale (De Jager & Vogt, 2010) because the RHT is based on a French Digital Elevation Model with a finer ~50-m resolution, is conditioned by detailed

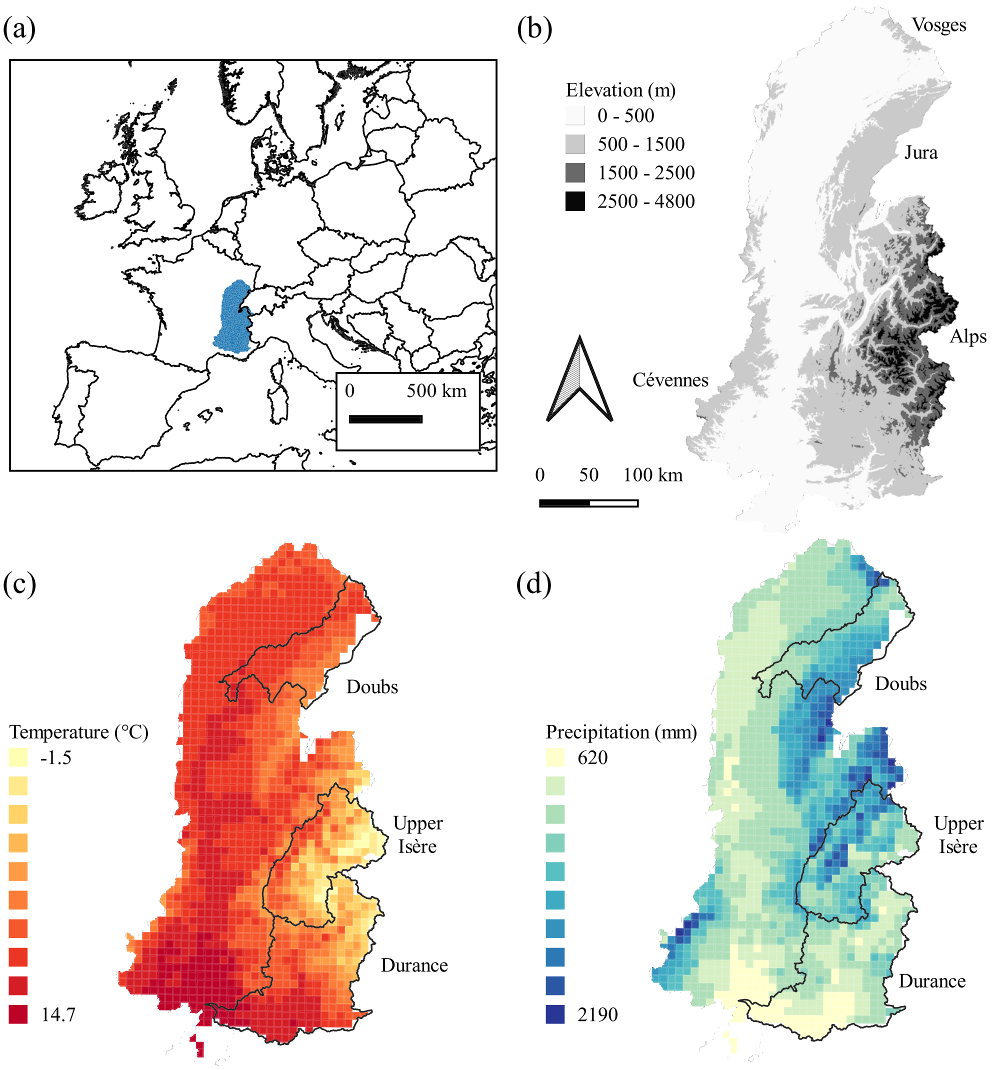

FIGURE 1 General location of the Rhône catchment in France (a). Elevation and main mountain ranges: Cévennes, Jura, Vosges and Alps (b). Mean air temperature (c) and precipitation (d) for the present period and locations of three sub-catchments used to describe our results

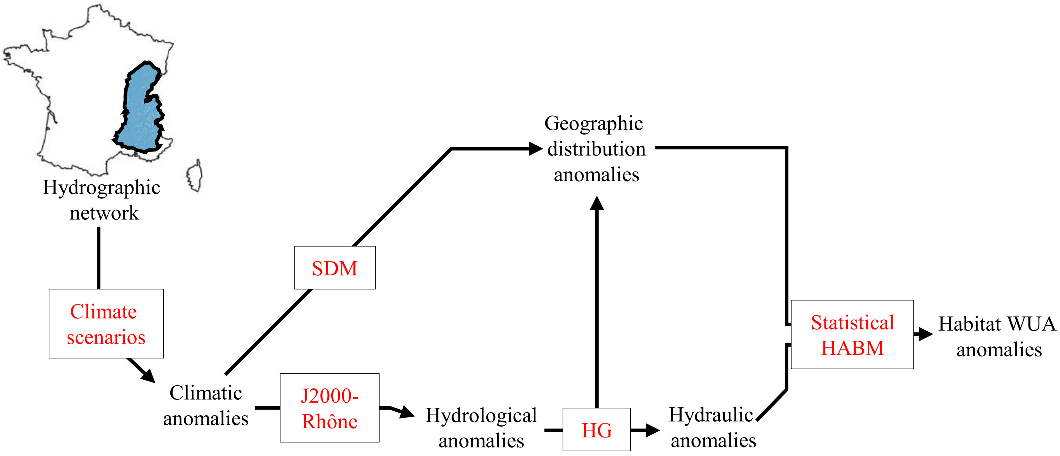

FIGURE 2 Graphical representation of the global logic of the modelling chain in this study. Modelling steps are in red colour. As detailed in Table 1, the output data of previous modelling steps were used as input data for some models. HG, hydraulic geometry; HABM, hydraulic habitat model; SDM, species distribution model; WUA, weighted usable area

French river maps and includes estimates of hydrological characteristics of reaches (Pella et al., 2012). Reaches of the RHT are segments between confluences with an average length of 2.5 km. Because the hydrographic network of the RHT physically starts when catchment areas reach 2.5 km^2 (Pella et al., 2012), it represents well small first-order streams. Several environmental characteristics (Table 1) were estimated on this network (Pella et al., 2012) and were used as input variables in the modelling chain. These included estimations of catchment area and mean slope of reaches from digital elevation models, distance to source along the river network, mean bed substrate size (Snelder, Lamouroux, & Pella, 2011) and interannual estimates of naturalized discharge statistics (e.g., median flow $Q50_{RHT}$) obtained by spatial extrapolations from gauging stations unimpacted by reservoir dams (Sauquet & Catalogne, 2011) (Table 1).

To illustrate how climate change could impact the habitat of species with different ecological requirements, we chose to develop HABM and SDM models for the life stages of three European fish species having contrasted hydraulic (Lamouroux & Capra, 2002; Plichard et al., 2020) and thermal requirements (Daufresne, 2008; Kottelat & Freyhof, 2007), and for which HABMs were available (Lamouroux & Capra, 2002). The adult resident brown trout (*Salmo trutta*; code TRF in Table 1) uses deep microhabitats and moderate water velocities (Lamouroux & Capra, 2002). It has the characteristic of cold and oxygenated European headwaters and is of high fishing interest. Sculpin (*Cottus gobio*, all sizes; code CHA in Table 1) selects microhabitats with intermediate current velocities but shallower water depths than trout (Plichard et al., 2020). It is present at lower elevations and lives in cold waters of medium-sized rivers. Adult barbel (*Barbus barbus*, longer than 22 cm; code BAF in Table 1) selects deeper and faster-flowing microhabitats than the two other species (Plichard et al., 2020). It is the typical species of larger, warmer streams (the 'barbel' zone; Huet, 1959).

2.3 | Climatic data

We extracted baseline climate data from the French near-surface SAFRAN meteorological reanalysis (Quintana-Seguí et al., 2008; Vidal et al., 2010), which provides spatially distributed daily mean temperature, precipitation and other atmospheric variables (at a resolution of 8 km × 8 km) over the study area during the present period considered here (1987 to 2012).

For the future climate (period 2075–2100), we considered two regional climate projections available from the CMIP5 (Coupled Model Intercomparison Project of the World Climate Research Programme; Taylor et al., 2012) modelling experiment, available on the DRIAS French portal (www.drias-climat.fr; Lémond et al., 2011). These two projections are derived from the French CNRM2014 experiment (Jouzel et al., 2014), which involves the French global climate model ARPEGE-Climat (Déqué et al., 1994) whose projections are downscaled over France by the regional model ALADIN-Climat (Colin et al., 2010). These projections consist of daily temperature, precipitation and atmospheric variables time series at the same spatial distribution as the SAFRAN reanalysis (8 km × 8 km resolution grid). The two projections used in this study correspond to Representative Concentration Pathways RCP4.5 and RCP8.5 (Jouzel et al., 2014) and encompass contrasting future climate conditions; RCP4.5 refers to an optimistic scenario (i.e., greenhouse gas emission declining around 2050 due to climate policy), and RCP8.5 refers to a pessimistic scenario (greenhouse gas emission continuously increasing without explicit climate policy).

Climatic anomalies in mean air temperature and mean precipitation were calculated for both projections as differences between the future and the present periods.

TABLE 1 Description of the variables involved in this study and their use as input variables for the models

Type of variable/code		Variable definition (unit)	Sources	Input variables used for		
				HG	SDM	HABM
Reach characteristics	*D*	Mean grain size (m)	RHT			x
	$Q50_{RHT}$	Median daily discharge ($m^3\ s^{-1}$) from the period between 1970 and 2008	RHT	x		
	S	Reach slope (m/km)			x	
	CA	Catchment area (km^2)	RHT		x	
	Dist_h	Distance to source along the flow network (km)	RHT		x	
HG parameters	$H50_{RHT}$	Reach average water depth at $Q50_{RHT}$ (m)	RHT	x		
	$W50_{RHT}$	Reach average wetted width at $Q50_{RHT}$ (m)	RHT	x	x	
	b	Width HG exponent (—)	RHT	x		
	f	Depth HG exponent (—)	RHT	x		
	H95	Reach-average water depth at *Q95* (m)	RHT			x
	W95	Reach-average wetted width at *Q95* (m)	RHT			x
Climatic variables						
	Tcold	Mean temperature of the coldest quarter (°C)	SAFRAN		x	
	Twarm	Mean temperature of the warmest quarter (°C)	SAFRAN		x	
	Tvar	Coefficient of variation of mean monthly temperature (%)	SAFRAN		x	
	Pwet	Cumulated precipitation of the wettest quarter (mm)	SAFRAN		x	
	Pdry	Cumulated precipitation of the driest quarter (mm)	SAFRAN		x	
	Pvar	Coefficient of variation of mean monthly precipitation (%)	SAFRAN		x	
J2000-Rhône results						
	Q95	Daily discharge exceeded 95% of the time ($m^3\ s^{-1}$)				x
SDM results						
	P_TRF	Theoretical presence of brown trout (—)				x
	P_BAF	Theoretical presence of barbel (—)				x
	P_CHA	Theoretical presence of sculpin (—)				x
HABM results						
	WUA_{TRF}	Weighted usable area (for 100 m of river length) for brown trout (m^2)				
	WUA_{BAF}	Weighted usable area (for 100 m of river length) for barbel (m^2)				
	WUA_{CHA}	Weighted usable area (for 100 m of river length) for sculpin (m^2)				

Note: (—) refers to dimensionless variables.

Abbreviations: HG, hydraulic geometry; HABM, hydraulic habitat model; SDM, species distribution model.

2.4 | The hydrological model of the catchment J2000-Rhône

J2000 is a distributed hydrological model (Krause et al., 2006) extensively used around the world (e.g., Branger et al., 2013; Fink et al., 2007; Firoz et al., 2018; Machado et al., 2016; Nepal, 2016; Nepal et al., 2014). The model represents the main hydrological processes in a simplified, yet physically sound way. It considers rain/snow partition and interception, evapotranspiration, snow accumulation and melting processes, infiltration in soils, surface runoff, groundwater recharge and routing in the hydrographic network. As a fully distributed hydrological model, it uses irregular hydrological response units (HRUs) as elementary modelling units (Flügel, 1995) on which the above-mentioned processes are calculated. Water flow is routed from HRU to HRU and then to the hydrographic network.

J2000-Rhône was set up for the French part of the Rhône River basin with the objective of assessing the impact of climate change and water management scenarios on the availability of water resources (Branger et al., 2016). The version of J2000-Rhône used for the present study considers only natural hydrological processes, that is, no anthropogenic features such as reservoir management operations, irrigation or drinking water uptakes, due to the difficulty of representing these anthropogenic alterations comprehensively over a large catchment. The input data for the model setup consist of a resampled

ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) Digital Terrain Model with 200-m resolution, the Corine Land Cover land use map from 2006 (https://land.copernicus.eu/pan-european/corine-land-cover), the European Soil Database map (https://esdac.jrc.ec.europa.eu/content/european-soil-database-v20-vector-and-attribute-data) and the French national 1:1,000,000 geological map (http://infoterre.brgm.fr/formulaire/telechargement-carte-geologique-metropolitaine-11-000-000). Land use, paedology and geology maps were re-classified in order to simplify the model parameterization. We considered 31 land use classes, 10 paedology classes and 17 geology classes on the whole Rhône catchment. The average HRU size was 5 km^2. Each HRU is related to a specific land use, paedology and geology class and the corresponding parameters.

We ran the model for the present and future periods using the above-mentioned climate forcings, with prior 30-year initialization runs. Forcings were assigned to each HRU based on the nearest SAFRAN cell. To calibrate the model, a set of 217 stations with limited water abstraction in their catchment was selected from the French national gauging network (http://www.hydro.eaufrance.fr/). Parameters were initially set according to prior information and the literature. The model was iteratively improved to better reproduce observed discharge rates while keeping the physical meaning of the parameters (Branger et al., 2016).

J2000-Rhône provides daily naturalized discharge time series for present and future periods and for every reach of its own hydrographic network. This hydrographic network was generated from the Digital Terrain Model during the HRU delineation process and was much coarser than the detailed (but more realistic) RHT network used by the HABM and SDM models. To extrapolate J2000-Rhône results on the RHT, we first associated each J2000-Rhône reach with its corresponding RHT reach, based on proximity and correspondence of upstream catchment areas. This allowed associating daily discharge data with 34% of RHT reaches. For RHT reaches without correspondence, we extrapolated discharge data from the nearest RHT reach with correspondence and situated downstream. These extrapolations of daily discharges were made following a proportionality assumption, using the ratio of the median flow $Q50_{RHT}$ (Table 1) of the two reaches.

Because low flow hydraulics have been successfully used to predict changes in fish assemblage structure (Lamouroux & Olivier, 2015), we decided to model hydraulic habitat suitabilities of fish species at $Q95$; the naturalized daily discharge exceeded 95% of the time. Accordingly, we checked how J2000-Rhône predicted observed low flow percentiles. Then, we derived $Q95$ quantiles for the present and future periods. These will be noted $Q95_{pre}$ and $Q95_{fut}$ throughout (and similarly for other variables in Table 1). Hydrological relative anomalies ($\Delta Q95$, in %) were defined as follows:

$$\Delta Q95 = \frac{Q95_{fut} - Q95_{pre}}{Q95_{pre}} \times 100. \tag{1}$$

2.5 | The HG model

Hydraulic translations of daily discharge data at each reach were made using the HG models of Morel et al. (2020). In brief, these models improve the classical HG relationships of Leopold and Maddock (1953). They are based on analyses of a unique collection of hydraulic data collected at the scale of stream reaches for 1327 reaches with limited morphological alteration in France and New Zealand (Morel et al., 2020). These models provide estimates of reach hydraulics at a given discharge rate in the absence of detailed field hydraulic measurements. They combine traditional formulations of 'downstream hydraulic geometry' (spatial variations in wetted width $W50_{RHT}$ and water depth $H50_{RHT}$ at median flow $Q50_{RHT}$) and 'at-a-reach hydraulic geometry' (temporal variations in wetted width W and water depth H with discharge rate Q). The resulting equations for predicting W and H are as follows:

$$H = H50_{RHT} \times [Q/Q50_{RHT}]^{f}, \tag{2}$$

$$W = W50_{RHT} \times [Q/Q50_{RHT}]^{b}, \tag{3}$$

where exponents f and b are 'at-a-station' HG exponents (Morel et al., 2020). Parameters of these models (b, f, $H50_{RHT}$ and $W50_{RHT}$) were themselves statistically predicted from several climatic, hydrologic, topographic and land use descriptors available over the RHT (Morel et al., 2020).

2.6 | Fish SDMs

The SDM is not the main focus of our approach and was used to constrain hydraulic habitat simulations to reaches where the species potentially occurred. Therefore, we adapted the approach of Grenouillet and Comte (2014) already used to predict climate change effects, and we used the same input variables (Table 1). However, we re-calibrated their SDM for our three illustrative fish species in the Rhône catchment and used our climatic data described above. The SDM predicts the probability of species occurrence in river reaches from reach- and catchment-scale environmental descriptors. Input variables (listed in Table 1) included reach median width, distance to source and catchment area (log-transformed and linearly combined in a single 'Up-down-gradient' variable, based on a PCA analysis) and reach slope. They also included the average, over years of the period considered (present period for fitting the model and future period for predictions), of annual climatic variables: mean air temperature of the coldest and warmest quarters, temperature variability, cumulated precipitation of the wettest and driest quarters and precipitation variability. These climate variables were untransformed and inherited at each RHT reach from the SAFRAN cell containing the longer part of the reach.

For re-calibrating the model (present period), we extracted fish data from national electrofishing databases compliant with European norms (BDMAP; Baglinière, 2018). We selected 558 sites sampled at least twice between 1985 and 2005 in the Rhône catchment, in order to reduce uncertainty on the occurrence of rare species. Fish presence–absence data were related to the environmental variables using an ensemble modelling approach (Araújo et al., 2005) based on different SDM corresponding to different modelling techniques: generalized additive models, multivariate adaptive regression splines, classification and regression trees, random forest and generalized boosted trees. Models were calibrated on 70% of the database while the remaining 30% were used for evaluation and threshold optimisation. Predictive performance was evaluated using the area under the receiver operating characteristics curves (ROC) method, giving the accuracy metric 'Area Under the Curve' (AUC) (Fielding & Bell, 1997). To take into account the variability introduced by the modelling method, we followed the procedure applied in Marmion et al. (2009) by averaging the probabilities of occurrence (weighted by AUC values) predicted by the five SDMs. Spatial and temporal autocorrelations were not accounted for in the approach of Grenouillet and Comte (2014). However, to reduce multicollinearity issues, the approach targeted parsimonious SDM with a reduced number of explanatory variables (little intercorrelated) but satisfactory predictive power (Buisson et al., 2010; Grenouillet et al., 2011). Variable importance in species x model combinations was calculated using the Pearson correlation between the predictions of the model involving all variables and the predictions of another model in which the variable of interest was randomly permuted among sites; importance was defined as (1—Pearson correlation).

Predictions were made using the average climatic variables over the years of the future period. We compared the predicted occurrence in current and future periods to identify reaches where the species should disappear, appear, remain present or remain absent. For this purpose, SDM predictions (probability of occurrence) were transformed into expected presence or absence using species-specific threshold values maximizing the sum of sensitivity and specificity (Manel et al., 2001). Statistical analyses for SDM were made using the R software library Biomod2 (Thuiller et al., 2009).

2.7 | The statistical fish HABMs

We used the statistical HABM of Lamouroux and Capra (2002) for estimating the hydraulic habitat suitability of adult brown trout, adult barbel and sculpin. These statistical habitat models upscale, at the reach scale, knowledge of hydraulic microhabitat selection by the three life stages (i.e., hydraulic 'preferences'). Hydraulic preferences of adult trout were expert adaptations for French rivers of North American models (Souchon et al., 1989). Hydraulic preferences of the other life stages were derived from observations in six French rivers of Southern France made over 8 years (Lamouroux et al., 1999). Plichard et al. (2020) confirmed a high degree of transferability of these microhabitat selection models between rivers, based on a larger data set collected in nine rivers.

HABMs predict a 'Weighted Usable Area' (WUA) in the reach for each specific life stage, at a given discharge rate, as a function of the HG of the reach (HG results) and an estimate of average particle size *D*. The WUA is the product of the reach wetted surface and a habitat value (HV) that varies between 0 and 1, depending on the suitability of microhabitat velocities and water depths in the reach for the species. In other words, WUA increases with both habitat quantity (wetted surface) and quality (HV). Here, we calculated WUA at *Q95* for the present and future periods, for brown trout, barbel and sculpin. A relative anomaly of habitat (ΔWUA, in %) is deduced:

$$\Delta WUA = \frac{WUA_{fut} - WUA_{pre}}{WUA_{pre}} \times 100. \tag{4}$$

Estimating habitat alteration only makes sense where the species is potentially present. This is where our SDM is used to constrain our HABM model (Figure 2). Therefore, for each species, we calculated hydraulic habitat anomalies only in reaches where SDM predicted its potential presence (in the present and/or future situation).

2.8 | Partial uncertainty assessment

Large-scale hydrological, hydraulic and habitat simulations are influenced by a wide variety of uncertainties, which correspond to each step of the modelling procedure (Figure 2) and propagate through the modelling chain. These include uncertainties of climate scenarios (partly illustrated by our use of two RCP scenarios), uncertainties of the climatic and hydrological models in the present situation and under future scenarios and uncertainties of the hydraulic translation of discharge values. Taking into account all sources of uncertainty in our simulations would be challenging if not impossible. For example, the uncertainties of hydrological alterations cannot be tested easily with field data, and their estimation obtained by running multiple hydrologic models would still be debatable.

Despite their complex estimation, elements on the uncertainties of large-scale simulations are needed for taking them into account in management decisions (e.g., reduction of abstraction). Here, we chose to do a partial and rough assessment of uncertainties, by estimating the potential combined effect of selected sources of uncertainties (on *Q95* and HG models), while not taking into account others whose consideration would be challenging (e.g., uncertainties on global climatic scenarios and on global J2000-Rhône structural hypotheses).

In practice, we ran the model chain of Figure 2 while adding simultaneously random uncertainties ($n = 100$ repetitions) on $Q95_{pre}$, $Q95_{fut}$ and HG models. These random uncertainties were assumed independent and were drawn from assumptions on error distributions. For *Q95* distribution error, we used the error distribution suggested by Lamouroux et al. (2014). Although this error distribution was originally developed for mean annual discharge in France (Lamouroux et al., 2014), the authors indicated how the error depended on discharge itself, justifying its use for other discharge statistics such as *Q95*. This choice of a discharge-dependent error makes sense for an application over the whole hydrographic network that contains many small rivers with low discharges and high relative uncertainty (as %) on their values. This led us to consider a normal error around log(*Q95*) with a standard deviation of (Lamouroux et al., 2014):

$$\sigma_{\log(Q95)} = 0.244 \times Q95^{-0.235}. \tag{5}$$

For errors on HG estimates, we used the data in Morel et al. (2020), which included leave-one-out-predictions of parameters $H50_{RHT}$, $W50_{RHT}$, f and b (Equations 2 and 3), and comparisons with field data. We retained factorial errors on these parameters with standard deviations:

$$\sigma_{\log(H50_{RHT})} = 0.308, \tag{6}$$

$$\sigma_{\log(W50_{RHT})} = 0.253, \tag{7}$$

$$\sigma_{\log(f)} = 0.499, \tag{8}$$

$$\sigma_{\log(b)} = 0.587. \tag{9}$$

3 | RESULTS

Mean air temperature increases over the whole catchment for both scenarios, with high anomalies for RCP8.5 (i.e., median anomaly of +4.2°C; Figure 3b) compared with RCP4.5 (median anomaly of +2.4°C; Figure 3a). Air temperature tends to increase more in some regions (e.g., in Doubs or in Durance sub-catchment). Most anomalies of annual precipitation are moderately negative, except locally in the Alps where both scenarios suggest combinations of increases and decreases (Figure 3c,d).

The hydrological model J2000-Rhône provides correct predictions of observed daily discharges (Branger et al., 2016), with a median Nash-Sutcliffe efficiency (Nash & Sutcliffe, 1970) of 0.51 and a median Kling-Gupta efficiency (Gupta et al., 2009) of 0.57. The reproduction of low flows is also satisfactory with an average relative difference of 6% for *Q90* (daily discharge value exceeded 90% of the time).

Predicted low flow (*Q95*) anomalies are highly heterogeneous over the catchment for both scenarios (Table 2 and Figure 3e,f). Some areas are negatively affected such as the Northern part of the catchment (e.g., the Doubs sub-catchment, where *Q95* is reduced by 60% and 30% under RCP8.5 and RCP4.5, respectively). Conversely, the Alps and a part of the Cévennes mountains demonstrate positive anomalies (e.g., a median increase of 10% and 22% in the Upper Isère sub-catchment under RCP8.5 and RCP4.5, respectively). SDM calibrations presented a high predictive performance with AUC values equal to 0.99 for trout (sensitivity = 98% of ‘true’ occurrence, 1-

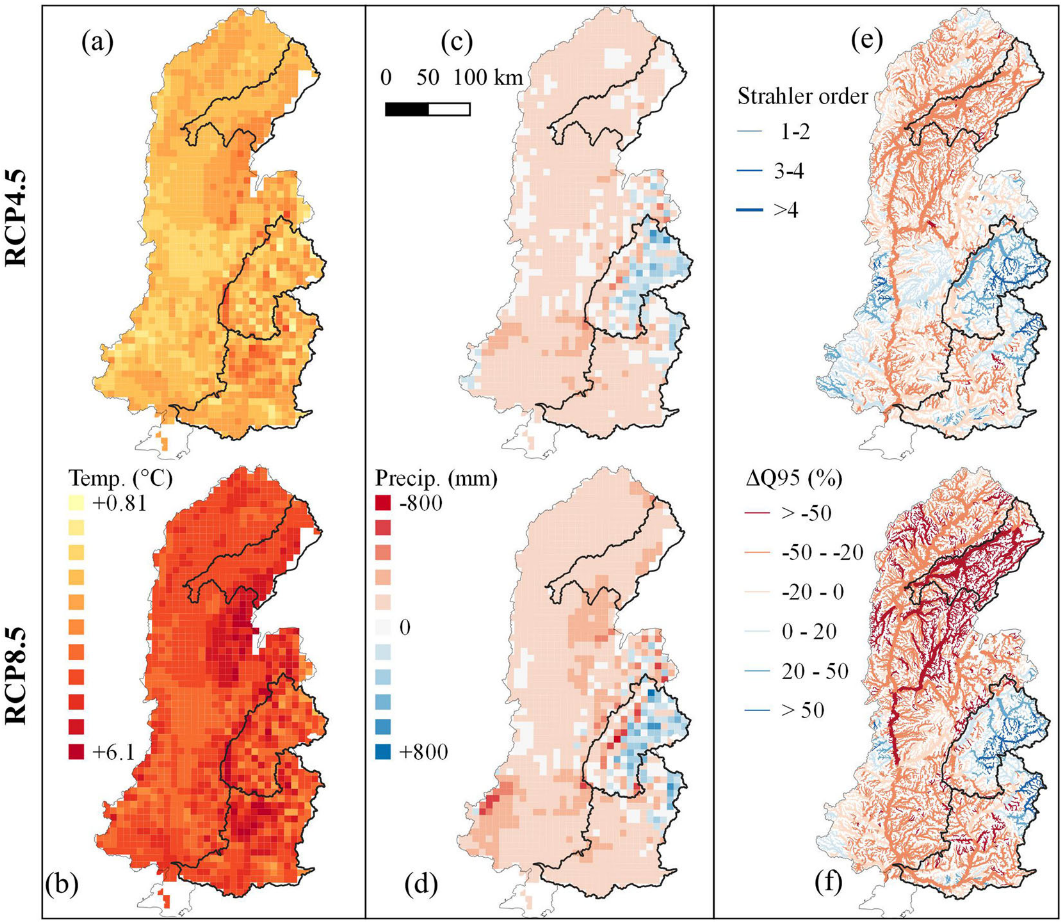

FIGURE 3 Estimated anomalies of mean temperature (a), (b); precipitation (c), (d); and relative anomalies of *Q95* (e), (f); under scenario RCP4.5 and RCP8.5, respectively

TABLE 2 Statistics (first quartile, median and third quartile, in %) of hydrological ($\Delta Q95$) and habitat (ΔWUA, for the three species) anomalies estimated on the whole Rhône catchment network and sub-catchments for both scenarios

	$\Delta Q95$		ΔWUA_{TRF}		ΔWUA_{CHA}		ΔWUA_{BAF}	
	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5
	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.	1st quart.; med.; 3rd quart.
Whole French part of the Rhône catchment	−27.5	−48.3	−6.7	−12.7	−11.2	−24.3	−8.0	−16.2
	−16.0	−38.6	−0.7	−3.9	−7.7	−18.7	−4.4	−10.7
	1.7	−18.8	0	0	−1.2	−11.0	−0.4	−6.4
Doubs	−40.1	−64.1	−12.4	−18.8	−12.4	−28.2	−13.6	−33.2
	−34.7	−60.1	−9.6	−15.8	−9.6	−23.7	−10.7	−17.8
	−30.4	−53.6	−6.9	−12.9	−6.9	−13.3	−6.1	−11.6
Upper Isère	−0.1	−19.5	0	−0.5	−7.9	−3.1	−7.9	−9.2
	22.3	10.3	0	0	−0.7	2.5	1.3	2.9
	38.8	37.4	6.1	5.6	6.8	8.5	9.4	14.8
Durance	−20.0	−41.0	−2.4	−7.1	−2.6	−15.2	−6.6	−15.3
	−9.6	−29.2	0	0	0	3.5	2.3	−9.9
	7.1	−0.0	0	0	0	17.1	11.9	−4.9

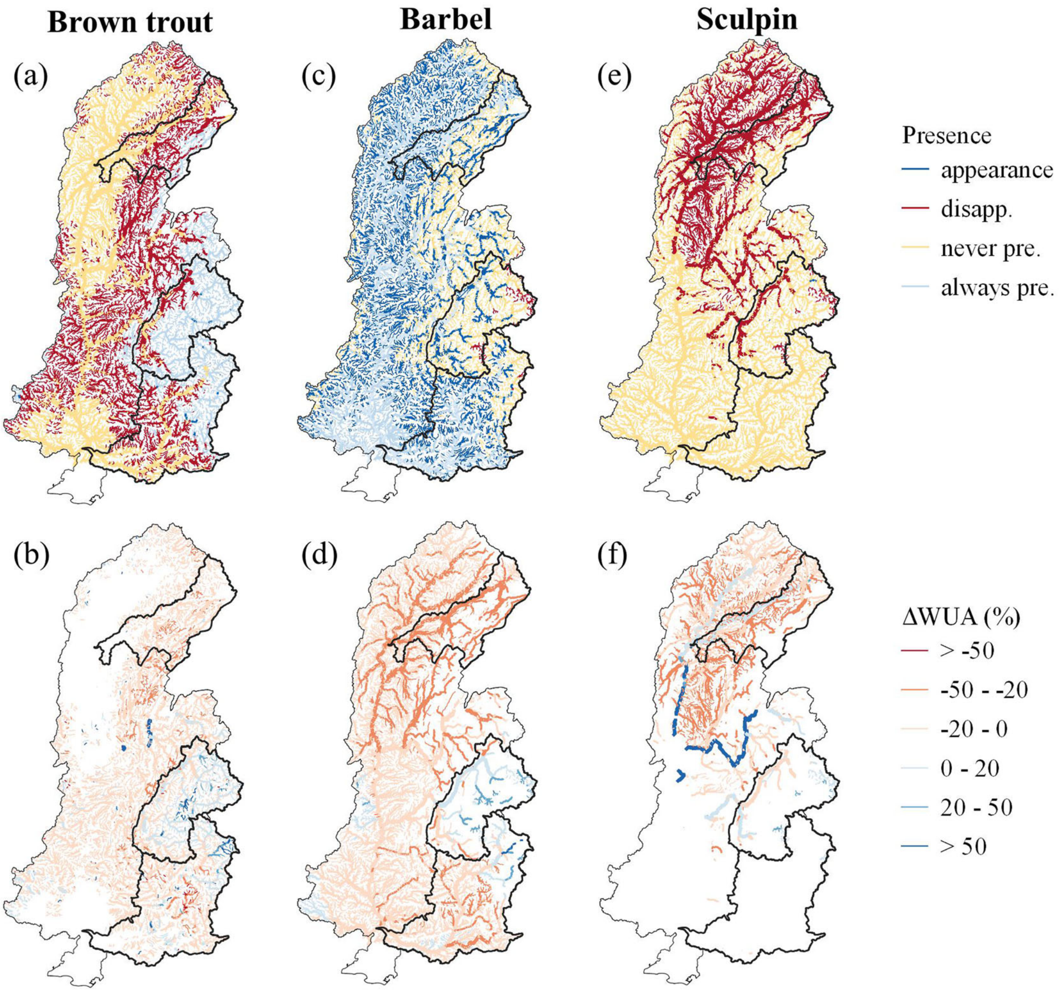

FIGURE 4 Change in theoretical presence and relative anomalies of *WUA* of brown trout (a), (b); barbel (c), (d); and sculpin (e), (f) under scenario RCP8.5

specificity = 0% of ‘wrong’ occurrence), 0.93 for sculpin (sensitivity = 94%, 1 - specificity = 21%) and 0.98 for barbel (sensitivity = 97%, 1 - specificity = 9%). Thresholds used to transform the predicted probability of occurrence of species into an expected presence or absence in the reach were 0.77, 0.60 and 0.37 for brown trout, sculpin and barbel, respectively. The statistical importance of each climatic explanatory variable varied strongly between models in the ensemble modelling approach (Figure S1). However, on average across models, climatic variables (temperature and precipitation) and reach characteristics had comparable importance in SDMs (Figure S1).

For the future period, SDMs predict important losses of geographical range for brown trout and sculpin under both scenarios. Brown trout could persist only in the cold mountainous areas under RCP8.5 and RCP4.5 (Figures 4a and 5a, to compare with the temperature map, Figure 1c). For sculpin, SDMs predict disappearance over the whole catchment under both scenarios with local exceptions in mountainous, colder areas of the Jura and in the Alps under RCP4.5 (Figures 4e and 5e). By contrast, barbel is currently present in the southern, lower and warmer part of the catchment and should extend its distribution towards upstream reaches under both scenarios (Figures 4c and 5c).

Hydraulic habitat anomalies have spatial patterns influenced by those of hydrological anomalies under both scenarios (Figures 4 and 5). Similarly to $\Delta Q95$, ΔWUA values present strong local variations for barbel and sculpin, with high negative ΔWUA where $Q95$ decreases importantly (e.g., the median ΔWUA_{BAF} and ΔWUA_{CHA} equal −17.8% and −23.7%, respectively, in the Doubs catchment under RCP8.5; Table 2) and moderate anomalies where $\Delta Q95$ is low (e.g., the median ΔWUA_{BAF} and ΔWUA_{CHA} equal 2.9% and 2.9%, respectively, in the Upper Isère catchment under RCP8.5; Table 2). Consequently, hydraulic habitats present more negative anomalies under RCP8.5 (Figure 4b,d,f) than under RCP4.5 (Figure 5b,d,f). Brown trout should be less impacted by hydrological changes than the two other species. For example, under the pessimistic scenario, median ΔWUA_{TRF}, ΔWUA_{BAF} and ΔWUA_{CHA} equal −3.9%, −10.7% and −18.7% over the whole catchment, respectively (Table 2).

Uncertainty simulations indicated that the uncertainties concerning the alteration of hydraulic habitat were very high at the reach scale (Figure 6a). On the other hand, when aggregated at the larger scale of sub-catchments, differences in habitat alteration were less influenced by uncertainties. Differences between sub-catchments (e.g., between Upper Isère and Doubs sub-catchments with,

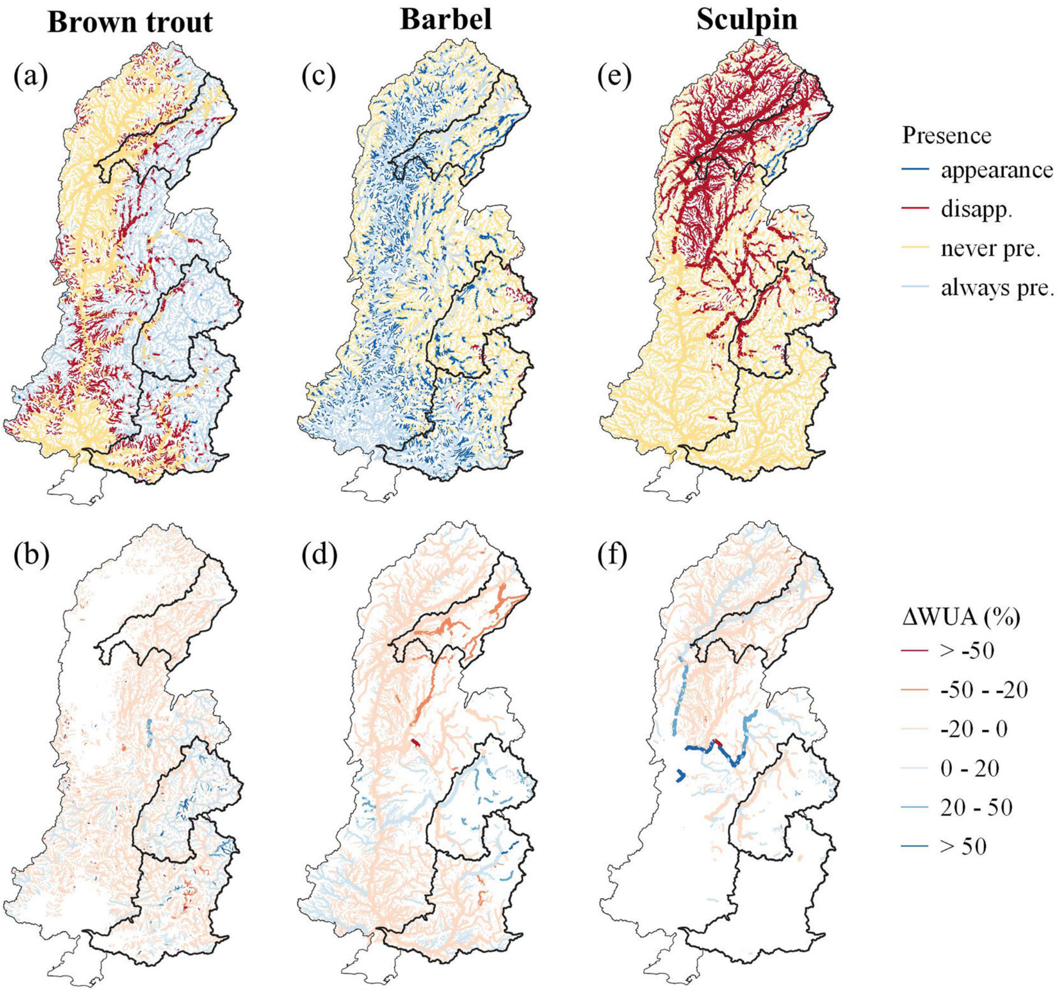

FIGURE 5 Change in theoretical presence and relative anomalies of *WUA* of brown trout (a), (b); barbel (c), (d); and sculpin (e), (f) under scenario RCP4.5

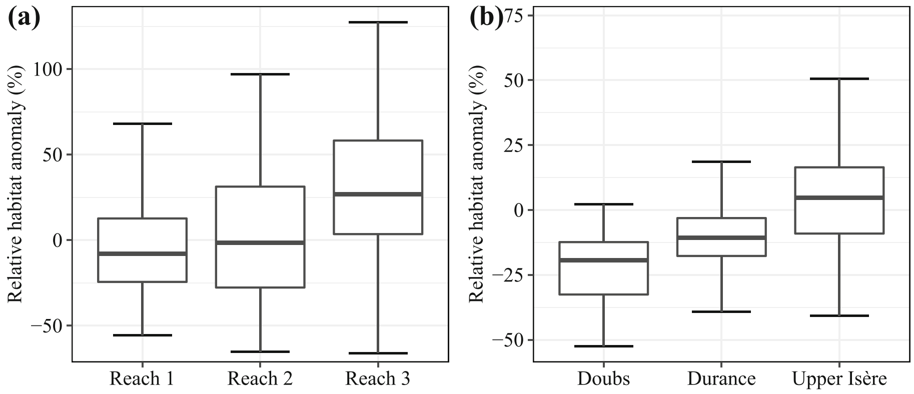

FIGURE 6 Under scenario RCP8.5: uncertainty on ΔWUA_{BAF} at three illustrative reaches (a), and uncertainty on median ΔWUA_{BAF} in three sub-catchments (b). Box plots correspond to $n = 100$ simulations with propagated uncertainties. The thick horizontal line indicates the median of the distribution, the box includes 50% of the data and the whiskers reach the highest and lowest value within 95% of the distribution. Differences between sub-catchments are less uncertain than differences between reaches. The three illustrative reaches were chosen for representing different levels of anomaly, a negative one for Reach 1 in Doubs catchment, to positive at Reach 3 in Upper Isère catchment with an intermediate situation at Reach 2 in Durance catchment.

respectively, median habitat alteration of 5.5% and −20.3% for WUA_{BAF} and scenario RCP 8.5) remain evident when uncertainties are propagated (Figure 6b).

4 | DISCUSSION

The climatic and hydrologic projections suggest strong environmental changes in the catchment, with (for RCP8.5) a median temperature anomaly of +4.2°C and spatially heterogeneous hydrological changes (median reduction of 38.6%). The heterogeneity of hydrological predictions corresponds to changes in the main drivers of the river flow regime. For example, in Jura, rivers are under karstic influences and experience severe low flows due to a limited groundwater storage. In such conditions, drier and warmer periods may generate more frequent and more severe droughts in summer. In the Alps, flow regimes controlled by snowmelt may shift to pluvial regimes. Higher temperatures will favour runoff processes causing higher discharges during the low flow period in winter (e.g., Milano et al., 2015).

Our results demonstrate that HABMs can provide a different information from that provided by SDMs, with HABM projections influenced by changes in river discharge and SDM results strongly driven by warming and with different expressions depending on species habitat requirements. Climate change could induce a 'double penalty' for sculpin and brown trout: SDMs show that these species should have a strong reduction in geographic distribution, and HABMs show that their hydraulic habitat suitabilities should be also reduced within their geographic distribution. However, the expected impacts are less dramatic for brown trout, which may find thermal refugees in the Alps according to SDM (Figure 4a) and whose hydraulic suitability is less reduced in medium to large streams according to HABM (Figure 4b). This is consistent with the preference of adult trout for lower velocities than sculpin (Lamouroux et al., 1999). In medium to large streams, discharge reductions can even generate more suitable hydraulic conditions for trout; warming will probably be the limiting environmental factor in these streams.

HABM and SDM projections are clearly opposite for barbel. SDMs reflect that warming should extend their distribution, whereas HABMs indicate that discharge reductions should decrease their hydraulic habitat suitability. Barbel is a rheophilic species using fast-flowing and deep microhabitats and is known to be strongly affected by discharge reductions (Lamouroux & Olivier, 2015). It is therefore likely that discharge reductions will prevent the extension of this species in many cases, even if temperature becomes more favourable. These differences illustrate the need to further combine SDMs and HABMs for providing more realistic projections of the ecological effects of climate change at large scales.

In our study, we linked HABMs and SDMs by making simulations of habitat suitabilities (HABMs) only where the species likely occurs (according to SDMs). This has a strong influence on HABM interpretation: For example, decrease in sculpin habitat suitability mostly concerns the North of the catchment because sculpin occurs (and will occur) less in the South. This demonstrates the importance of interpreting habitat simulations in a wider ecological context, which was not always done in previous HABM applications at large scales (Damiani et al., 2019). Incorporating directly the effect of hydraulic habitat changes in SDM construction would be attractive but remains currently challenging. First, most current SDMs predict species occurrence, while HABMs predict changes in habitat suitability and potential effects on abundance. Therefore, further combining HABMs and SDMs would require using SDMs that account for abundance data. Second, and more importantly, as long as SDMs are calibrated in space, they will mostly reflect responses to strong spatial environmental gradients in catchments such as longitudinal environmental gradients (Huang & Frimpong, 2016). This interpretation is reinforced by the fact that variable importance varied strongly among models in our ensemble modelling approach, that is, SDMs may not reflect the pure effect of each explanatory variable. Improved combinations of SDMs and HABMs would require calibrating these models based on observed temporal changes in species distribution and abundance, that is, using temporal rather than spatial calibration. Although SDMs have been used to predict temporal changes (as here), long-term abundance data collected in multiple sites are still lacking for calibrating SDMs based on observed temporal changes. It is possible, however, to test the inclusion of more hydrological (e.g., Wenger et al., 2010) and hydraulic variables (HG and HABM outputs) in current SDMs.

Our work remains a methodological exercise at this stage because catchment-scale models inevitably suffer from many limits. Although we tried to address uncertainty issues, they were not fully accounted for. Concerning the hydrological component, for example, there are identified biases of the SAFRAN reanalysis used as climate forcing during the present period, in particular in mountainous regions where precipitation can be significantly underestimated. A way forward would be to use other climate reanalyses more suited to mountain areas such as SPAZM (Gottardi et al., 2012). Moreover, it is well known that climate projections present a high level of uncertainty, which is enhanced by the use of model chains (global climate model run with different initial conditions, disaggregation and bias correction methods and catchment hydrological models), and thus provide quite uncertain discharge estimates. The recommended strategy to avoid this (or at least to assess the level of uncertainty associated with the hydrological outputs) is to perform multiple simulations, including numerous hydrological models (Vidal et al., 2016). More generally, the realism of our hydrological approach could be strongly improved by accounting for river regulation (reservoir management operations and irrigation or drinking water uptakes).

The biological components of our approach, HABM and SDM models, were partly validated from field observations but also have strong limits and uncertainties (Comte & Grenouillet, 2015; Lamouroux & Olivier, 2015) and use input variables that are uncertain themselves. Our biological models do not account for the impacts of proximate habitat variables other than hydraulics, such as water temperature (Beaufort et al., 2016) or nutrient fluxes (Dupas et al., 2013). In particular, water temperature models would be very valuable to use in large-scale approaches as done in site-specific ones (Muñoz-Mas et al., 2016), because temperature may be locally heterogeneous in the hydrographic network with the influence of tributaries, groundwater sources or shading (Beaufort et al., 2020). By providing patches of cold water necessary for some species and life stages, local thermal refugia can help fish assemblages to cope with global warming (Fullerton et al., 2018). The multiple sources of uncertainty of our approach could be further investigated, for example, by analysing differences among results of the various SDM sub-models, by accounting for spatial and temporal autocorrelation in SDMs or by developing HABM models for other sources of habitat preference information (e.g., Martínez-Capel et al., 2009), other specific size classes or other biological groups than fish (and covering a wider range of habitat requirements). Evidently, accounting for the uncertainty of biological responses to environmental changes is challenging, given the complexity of population dynamics and the potential influence of many factors not accounted for here (e.g., population adaptations, biological interactions such as competition and predation, and water quality issues).

Although based on a single distributed hydrologic model, and although our partial uncertainty analysis shows that any reach-scale interpretation would be speculative, our results illustrate that climate change may have very heterogeneous local expressions in the future, at least in mountainous regions (Christensen et al., 2008). For example, as opposed to the Upper Isère sub-catchment, the Doubs sub-catchment seems to be more affected by climate change. This illustrates that management measures in response to climate change may need to be rapid, context-dependent and local.

5 | CONCLUSION

Despite strong uncertainties, our approach demonstrates the limitations and the combined relevance of HABMs and SDMs for obtaining improved predictions of the ecological effects of climate change. Repeating simulations combining both models with various hydrological and biological models and in different climatic regions is needed, for managers to assess the potential solutions they can implement (e.g., changes in water abstraction, environmental flow implementation, restoration of groundwater–surface water connectivity, conservation of thermal refugia and barrier removals for facilitating population resilience). Because the impacts of climate change will likely be heterogeneous in large catchments, our approach can contribute to identifying areas (such as the Doubs sub-catchment) where action should be particularly anticipated.

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CONFLICTS OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Nicolas Lamouroux and Maxime Morel conceived the ideas and designed methods; Hervé Pella and Nicolas Lamouroux provided HABM data; Eric Sauquet, Flora Branger and Isabelle Braud provided J2000 data; Gaël Grenouillet and Jessica Côte provided SDM data; Maxime Morel analysed the data; Maxime Morel and Nicolas Lamouroux led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SIGNIFICANCE STATEMENT

Most studies predicting the impacts of climate change on fish in river catchments rely on SDMs. SDMs do not account for the effects of proximate habitat variables such as microhabitat hydraulics. This study tests the use of HABMs in river catchments for predicting the impacts of climate change. HABMs focus on the effect of microhabitat hydraulics on fish habitat suitability. We compare how SDMs and HABMs estimate the biological impacts of climate change scenarios in a large catchment. Results show that SDMs and HABMs can provide different responses to climate change. We discuss their complementarity.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created in this study.

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