Brown trout thermal niche and climate change: expected changes in the distribution of cold-water fish in central Spain

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ABSTRACT

This paper addresses the determination of the realized thermal niche and the effects of climate change on the range distribution of two brown trout populations inhabiting two streams in the Duero River basin (Iberian Peninsula) at the edge of the natural distribution area of this species. For reaching these goals, new methodological developments were applied to improve reliability of forecasts. Water temperature data were collected using 11 thermographs located along the altitudinal gradient, and they were used to model the relationship between stream temperature and air temperature along the river continuum. Trout abundance was studied using electrofishing at 37 sites to determine the current distribution. The Representative Concentration Pathways RCP4·5 and RCP8·5 change scenarios adopted by the International Panel of Climate Change for its Fifth Assessment Report were used for simulations and local downscaling in this study. We found more reliable results using the daily mean stream temperature than maximum daily temperature and their respective 7 days moving average to determine the distribution thresholds. Thereby, the observed limits of the summer distribution of brown trout were linked to thresholds between 18·1 and 18·7 °C. These temperatures characterize a realized thermal niche narrower than the physiological thermal range. In the most unfavourable climate change scenario, the thermal habitat loss of brown trout increased to 38% (Cega stream) and 11% (Pirón stream) in the upstream direction at the end of the century; however, at the Cega stream, the range reduction could reach 56% due to the effect of a 'warm-window' opening in the piedmont reach.

INTRODUCTION

Temperature has a large influence on the biological success of fish and other aquatic organisms (Nukazawa *et al.* 2011), acting as a fundamental driver affecting the energy budget, growth (Elliott *et al.* 1995; Elliott and Hurley 1999, 2001; Forseth *et al.* 2009; Elliott and Allonby 2013) and other physiological functions of fish (Jeffries *et al.* 2012; Warren *et al.* 2012; Lahnsteiner and Leitner 2013; Vornanen *et al.* 2014), such as ecological relationships (Hein *et al.* 2013; Fey and Herren 2014) and even 'personality' (Frost *et al.* 2013). Temperature is a component of the ecological niche, and it is named 'thermal niche' (consolidated term in bibliography: e.g. Magnuson and Destasio 1996; Wehrly *et al.* 2003; Angilletta 2009; Finstad *et al.* 2011).

Spotila *et al.* (1989) defined physiological niche as the set of environmental conditions under which a species can persist (cf. Hutchinson 1957; Leibold 1995). 'Persist' means that $dN/dt > 0$ (May and McLean 2007). The temperature range at which the brown trout has a positive somatic growth was established by several works (3·6–19·5 °C in Elliott *et al.* 1995; approximately 5–23 °C in Forseth *et al.* 2009). This range of thermal efficiency is closely linked to the fundamental physiological niche for thermal conditions (fundamental thermal niche) (Angilletta 2009) for brown trout. This range must be at most equal to the tolerance range of temperatures as defined by the temperatures of incipient lethality [0–25 °C, approximately (Elliott and Elliott 2010)]. The general approach for thermal niche as defined by Magnuson and Destasio (1996) (the preferred temperature ±5 °C, accepting that fish spend all their time within this interval) seems to approach to the realized niche better than to the wider fundamental thermal niche. Nonetheless, the optimal growth temperature is influenced by fish uptake and fish size. Forseth and Jonsson (1994) reported that the optimal growth temperature for fish eating brown trout was 16 °C, which is higher than that found for trout fed with pellets (average: 13·5 °C, Forseth *et al.* 2009) or invertebrates (average: 13·1 °C

Elliott *et al.* 1995). On the other hand, the optimal temperature changes with fish size (Handeland *et al.* 2008, Morita *et al.* 2010). Thus, it is not straightforward to give one figure for optimal temperature for growth in a species.

Stream temperature is strongly correlated with air temperature (Edinger *et al.* 1968; Mohseni *et al.* 1998; Bogan *et al.* 2003; Caissie 2006), and an increase in temperature due to global warming can dramatically disturb aquatic ecosystems (Wade, 2006; Woodward *et al.* 2010). Climate change has the potential to increase or decrease habitat availability (Hughes 2000, Parmesan 2006). By this reason, the distribution of cold-water species such as brown trout and other salmonids is likely to suffer a displacement in the lower limits of their range to higher altitudes and latitudes (i.e. Crozier *et al.* 2008, Beer and Anderson 2013, Ruesch *et al.* 2012, Eby *et al.* 2014). The simulation of climate scenarios can help us assess the magnitude of the loss of suitable habitat ranges, not only in terms of the distribution range but also in terms of the physiological efficiency (i.e. Hari *et al.* 2006; Jonsson and Jonsson 2009; Wenger *et al.* 2011; Ayllón *et al.* 2013). According to Haldane's second hypothesis (Haldane 1956), these losses are more likely to be noticed at the limits of the thermal axis of the species' ecological niche. This is the case for several Iberian populations of brown trout, which inhabit the southern edge of the native distribution of this species.

The variation of the thermal regime, similar to other physical variables, is a continuum within a given stream network that tracks the geographical and physiographical changes along the network (Vannote *et al.* 1980). To represent this continuum, modelling can be a useful tool. Many deterministic, regressive and stochastic models have been developed to relate both air temperature and stream temperature. Deterministic models use an energetic budget to forecast stream temperature (Theurer *et al.* 1984; Evans *et al.* 1998), whereas regressive and stochastic models mainly use the relationship with air temperature to predict stream temperature (Caissie *et al.* 1998, St-Hilaire *et al.* 2011). Although deterministic models have a high explanatory strength, regressive and stochastic models may also exhibit high predictive power. Moreover, the type of data needed by the deterministic models is much harder to collect than the data needed by the regressive and stochastic models. Meteorological services have a large amount of spatial and temporal information on air temperature, which makes this variable very attractive for forecasting future stream thermal behaviour from climatic models.

The aim of this study is to quantitatively describe the influence of temperature on trout distribution along streams and determine how it is affected by climate change. For this purpose, we empirically determined the threshold temperature that characterizes the distribution limits of trout in the study area. We selected the best predictor among different expressions of temperature, namely the daily mean temperature for 7 consecutive days (studied as a series, not averaged), the weekly moving average of daily mean temperatures, the daily maximum temperature for 7 consecutive days and the weekly moving average of daily maximum temperatures. Next, we adopted the best indicator to create projections based on the latest climate change scenarios (Taylor *et al.* 2009, adopted by IPCC 2013). In this study, global climate models (which have coarse resolution) were transformed to a local scale using a statistical downscaling method to obtain the local outcomes. We continuously modelled the stream temperature throughout the length of the streams at a daily resolution and then simulated the change of the thermal habitat. Our methodology aims to decrease the necessary steps to reach this goal by reducing the statistical uncertainty.

MATERIALS AND METHODS

Study site

Fieldwork was conducted in two tributaries of the Duero River [Cega and Pirón streams (40°59′N; 3°50′W), central Spain]. The Cega and Pirón streams are 135 and 92 km long, respectively. The Pirón stream is the main tributary of the Cega stream. There is only one major dam in Pirón (Torrecaballeros dam; capacity: 0·324 hm^3; maximum depth: 26 m; altitude: 1390 m a.s.l.), and there are no dams in Cega that are able to significantly alter the flow regime. Granitic meta-detritic geology dominates the headwater basins. A karst belt occurs in the piedmont zone, giving way to large sand flatlands of detritic-tertiary origin with detritic-quaternary alluvial deposits.

Gauging stations 2016 and 2714 (official network codes; at 938 and 838 m a.s.l., respectively) in the Cega stream and 2057 (869 m a.s.l.) in the Pirón stream were used to characterize the hydrological regime of both streams. Snowmelt and winter–spring rainfall are important in these basins. Thus, an 'extreme winter' becomes an extended 'moderate winter' (Haines *et al.* 1988). Dry summers and permeability in flatlands cause the appearance of dry reaches in channels of the Cega and Pirón streams. The annual runoff averages of the last 20 years (to 2011) were 88·6 and 34·3 hm^3 at stations 2016 and 2057, respectively. Gauging station 2714 began to operate in 2004, and the annual runoff average in 2011 was 52 hm^3 (MAGRAMA 2014).

Data collection and testing

Observed maximum and minimum air temperatures were obtained from AEMET (Spanish Meteorological Agency) station number 2516 in Ataquines. This meteorological station was selected because it is the closest to the stream

temperature sites (average 69 km) and has the best data series to fit the models and simulate climate change scenarios. When properly chosen, a relatively large distance (up to 244 km in Mohseni *et al.* 1998) from the river to the meteorological stations does not negatively affect the strength of the water–air relationship (Pilgrim *et al.* 1998). Before selecting the data, air temperature data were tested to assess their reliability by applying a homogeneity test. This test is based on a two-sample Kolmogorov–Smirnov test, and it marks years as possibly inhomogeneous data. In a second phase, the marked years are matched against the distribution of the entire series to determine if they have true inhomogeneities, searching for possible dissimilarities between the empirical distribution functions. Consequently, only data before 1955 were discarded.

Water temperature was registered every 2 h using Hobo® Water Temperature Pro v2 (Onset®) thermographs located at 11 sites along the altitudinal gradient of the trout range in both streams [six sites in the Cega stream (Ct1 to Ct6) and five sites in Pirón stream (Pt1 to Pt5) (Figure 1, Table I)] between April 2011 and October 2012. The reaches where the Ct4 and Pt5 thermographs were placed were temporarily dry in 2011.

Electrofishing was conducted at 37 sites [C1 to C25 sites from 1610 to 730 m a.s.l. in the Cega stream and P1 to P12 sites from 1620 to 786 m a.s.l. in the Pirón stream (Figure 1, Table I)] in August for two consecutive years (1997 and 1998) to characterize trout populations. Average distance between consecutive sites was 4·45 km (range: 0·55–12·06 km) at Cega stream and 6·36 km (range: 2·46–12·30 km) at Pirón stream. Density was obtained for trout and the rest of present fish species by means of the maximum weighted likelihood method (Carle and Strub 1978). A severe drought occurred in 1998, and as a result, sites C7, C11, C14, C22, C23, P3 and those downstream of P10 were dry during the second electrofishing sampling event.

Table I. Altitude of electrofishing sites at Cega stream (C*n*) and Pirón stream (P*n*).

Cega stream		Pirón stream	
Site	Altitude	Site	Altitude
C1	1610	P1	1620
C2	1320	P2	1337
C3	1258	P3	969
C4	1150	P4	908
C5	1106	P5	879
C6	1044	P6	858
C7	995	P7	856
C8	966	P8	835
C9	961	P9	822
C10	944	P10	810
C11	934	P11	804
C12	921	P12	786
C13	910		
C14	898		
C15	885		
C16	866		
C17	845		
C18	805		
C19	798		
C20	788		
C21	780		
C22	778		
C23	762		
C24	748		
C25	730		

n is the site number. Unit: m a.s.l.

Water temperature at the electrofishing time was rebuilt by modelling as explained later. The drought that occurred in 1998 did not negatively affect to study reliability, quite the contrary: drought is a singularity that introduces useful variability to the analysis.

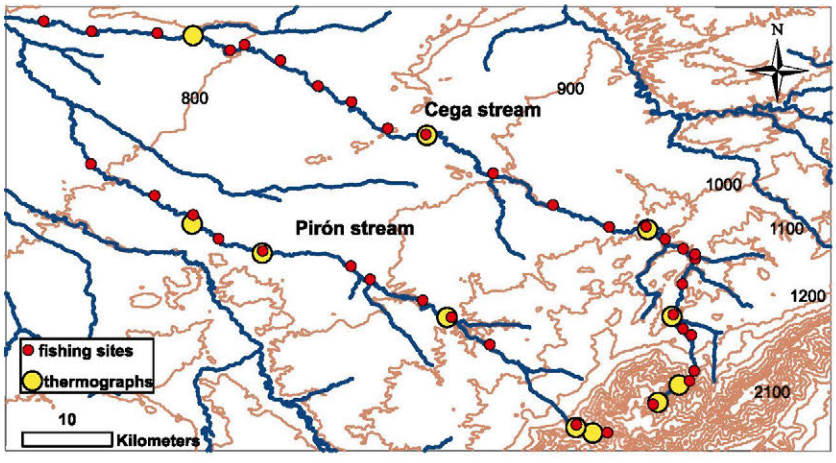

Figure 1. Location map of thermographs and electrofishing sites. Distance between contour lines (altitude above sea level): 100 m. Thermographs are numbered in text from headwaters to downwaters, Ct1 to Ct6 (Cega stream) and Pt1 to Pt5 (Pirón stream). Electrofishing sites are numbered from headwaters to downwaters, C1 to C25 (Cega stream) and P1 to P12 (Pirón stream).

Climate change modelling and downscaling

We used data from nine global climate models associated with the 5th Coupled Model Intercomparison Project (Table II). For these models, we used a 'twentieth century' simulation as the control run (the Historical simulation) and two future climate projections corresponding to the Representative Concentration Pathways RCP4·5 (stable scenario) and RCP8·5 (more increasing scenario) (Taylor *et al.* 2009).

For downscaling, we used a two-step analogue statistical method developed by Ribalaygua *et al.* (2013). The first step is an analogue approach (Zorita and von Storch 1999) in which the most similar number (n) of days to the day to be downscaled is selected. The similarity between the two days was measured using the pseudo-Euclidean distance between four large-scale fields as predictors: 1 the speed and 2 direction of the geostrophic wind at 1000 hPa and (3) the speed and (4) direction of the geostrophic wind at 500 hPa. In the second step, the temperature determination was obtained using a multiple linear regression analysis using the selected n of most analogous days. This was performed for each station and for each problem day, as well as for maximum and minimum temperatures. The linear regression uses forward and backward stepwise selections of the predictors to select only the predictive variables for that particular case.

As a measure of the goodness of the downscaling methodology, Figure 2 shows the monthly average of the maximum and minimum daily air temperatures for the observed data series (1958–2002) and for the simulated maximum and minimum values by downscaling the European Centre for Medium-Range Weather Forecasts ERA-40 re-analysis of daily data (Uppala *et al.* 2005). Bias and mean absolute error (MAE) were used as goodness indicators, and the means of their monthly averages of maximum values were −0·03 and 1·77 °C, respectively. The means of the monthly averages of minimum values were −0·05 and 1·88 °C, respectively. These values represent very good values, particularly for MAE, if we consider that the attributable error to the meteorological stations is approximately 1 °C.

A systematic error is obtained when comparing the simulated data from climate models with the observed data from reference time series due to the inherent downscaling methodology error and to the inner global climate model error (which usually introduce a bias over the data). To correct this systematic error, the future climate projections were corrected according to a parametric quantile–quantile method (Monjo *et al.* 2014). This was performed by comparing the observed and projected empirical cumulative distribution functions (ECDFs), linking them by the ECDF of the downscaled ERA-40.

As a consequence, daily maximum and minimum temperatures for the Ataquines meteorological station were obtained for each climate change scenario. From these temperatures, daily mean temperatures were obtained and used as an input to simulate climate change scenario effects on the Cega and Pirón streams. Figure 3 shows the quarterly increasing trends of simulated daily mean air temperature (DMAT).

Stream temperature modelling

Modelling was necessary to rebuild the stream thermal data because stream temperature measurements and fishing samplings did not overlap in time. Water temperature follows air temperature with a small time lag. Therefore, weekly moving average stream temperature is often used for this purpose because it usually exhibits a better correlation than the daily average (Stefan & Preud'homme 1993). On the other hand, the established time for determining thermal tolerance is usually 7 consecutive

Table II. The nine CMIP5 climate models used in this study.

Model	Institution	Country	Resolution (lon × lat)
BCC-CSM1-1	Beijing Climate Center (BCC), China Meteorological Administration	China	2·8 × 2·8°
CanESM2	Canadian Centre for Climate Modelling and Analysis (CC-CMA)	Canada	2·8 × 2·8°
CNRM-CM5	Centre National de Recherches Meteorologiques/Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique (CNRM-CERFACS)	France	1·4 × 1·4°
GFDL-ESM2 M	Geophysical Fluid Dynamics Laboratory (GFDL)	United States	2 × 2·5°
HADGEM2-CC	Met Office Hadley Centre (MOHC)	UK	1·87 × 1·25°
MIROC-ESM-CHEM	Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Atmosphere and Ocean Research Institute (AORI), and National Institute for Environmental Studies (NIES)	Japan	2·8 × 2·8°
MPI-ESM-MR	Max Planck Institute for Meteorology (MPI-M)	Germany	1·8 × 1·8°
MRI-CGCM3	Meteorological Research Institute (MRI)	Japan	1·2 × 1·2°
NorESM1-M	Norwegian Climate Centre (NCC)	Norway	2·5 × 1·9°

More details can be found in http://cmip-pcmdi.llnl.gov/cmip5/

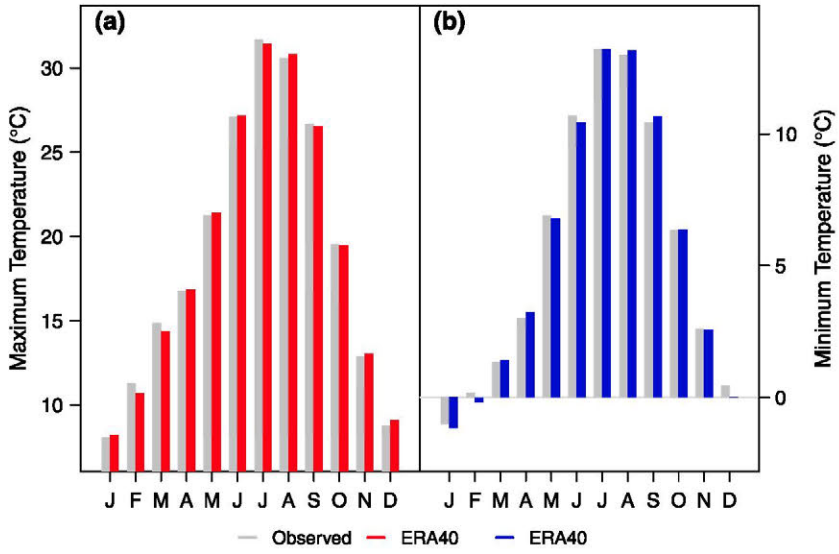

Figure 2. Monthly average of (a) maximum and (b) minimum daily air temperatures for the observed data series (1958-2002) and for the simulated maximum and minimum values by downscaling of the ERA-40 re-analysis.

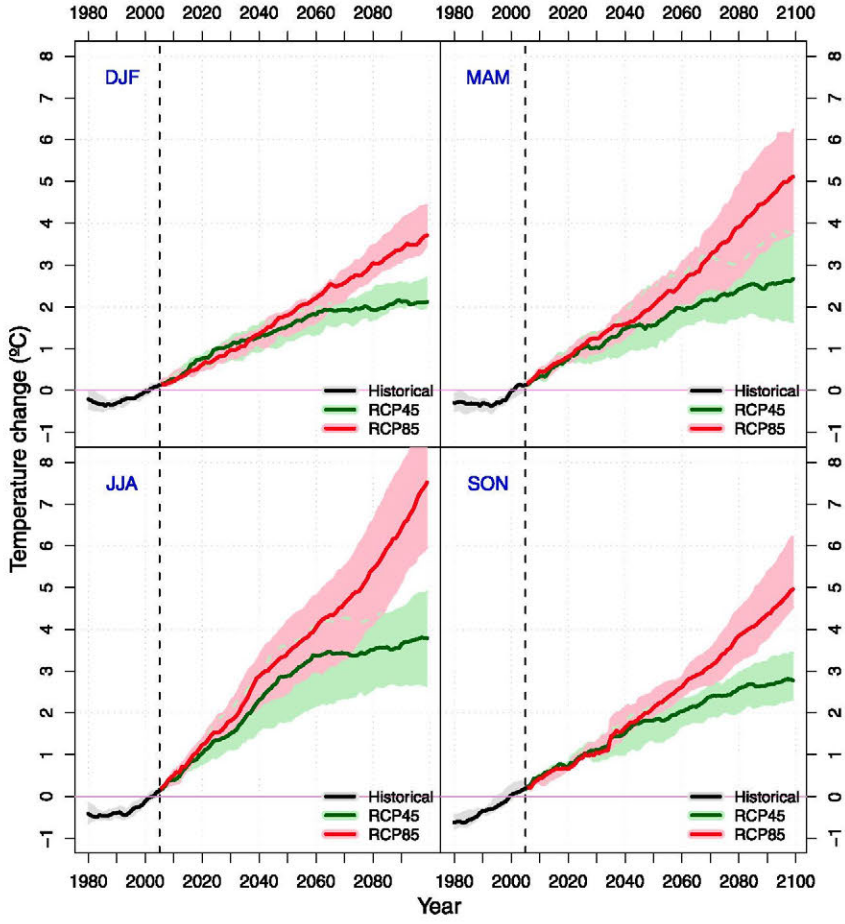

Figure 3. Expected relative seasonal increases in daily mean temperature throughout the 21st century (as 30-year moving averages) for the two studied RCPs (RCP4·5 and RCP8·5) against the 1971–2000 average (used as a reference). The vertical dotted line indicates the end of the historical experiment (black) and the start of the (November) RCPs. Thick lines show the median of the values for all models; the shaded area indicates ranges from the 10th to 90th percentiles. Seasons are indicated by their months: (a) winter (December, January, February); (b) spring (March, April, May); (c) summer (June, July, August); (d) autumn (September, October).

days (Elliott and Elliott 2010). However, using the weekly moving average could introduce errors such as the overestimation of the importance of a threshold because a determined weekly moving average does not indicate that every considered daily average was equal to or higher than the weekly moving average. Consequently, daily mean temperature was used in this study because it better reflects the average conditions that trout must experience for an extended period. In addition, studying events of 7 consecutive days above a daily mean threshold was preferred over using the 7-day moving average because it better reflects when a threshold is exceeded. We therefore needed to improve the correlation between air and water daily temperatures and used a modification of the Mohseni *et al.* (1998) model to accomplish this. This modified model includes a trajectory of temperature by adding the product of the daily increase in daily mean temperature and a parameter reflecting the resistance of water temperature to change.

The original Mohseni *et al.* 1998 model is as follows:

$$T_s = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - T_a)}} \quad (1)$$

where T_s is daily mean stream temperature (DMST), T_a is DMAT, μ is the estimated minimum stream temperature, α is the estimated maximum stream temperature, β represents the air temperature at which the rate of change of the stream temperature with respect to the air temperature is at a maximum and γ is the value of the rate of change at β.

The introduced trajectory component modifies the model to

$$T_s = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - T_a)}} + \lambda(\Delta T_a) \quad (2)$$

where λ is a coefficient representing the resistance of DMST to change with respect to DMAT variation in one day (ΔT_a).

Nonlinear regression was used to estimate the parameters of the models, and bootstrap techniques were used to consider the autocorrelation effect on the parametric signification (Freedman and Peters 1984). Calculations were performed using R software (R Core Team 2013). A 95% confidence interval was calculated for each parameter. Bayesian information criterion (BIC), Akaike information criterion (AIC) and root mean square error (RMSE) were used to test the modified model.

High correlation was detected between the annual average of DMST and altitude in both streams ($R^2 = 0{\cdot}986$ and $0{\cdot}985$). Thus, altitudinal interpolation of the model parameters was performed to determine the values of the estimated parameters at each electrofishing site; altitudinal extrapolation was performed for the C23, C24 and C25 sites in the Cega stream and for the P11 and P12 sites in the Pirón stream. A digital elevation model [DEM at a 5-m resolution, obtained from LIDAR, IGN (National Geographic Institute of the Spanish Government)] was used for modelling stream temperature as a continuum. Thus, the obtained models were used to study the electrofishing sites with the different sampling dates and climate change scenarios. Thereby, it was possible to reflect thermal heterogeneity, and the proportion of thermal habitat loss was determined continuously all along the stream with high spatial resolution. ArcGis® 10·1 (by ESRI®) was used to manage the DEM.

Thermal threshold determination

The number of days that exceeded different thresholds of daily mean temperature at electrofishing sites between 1997 and 1998 was quantified. The number of times that the thresholds were exceeded for 7 consecutive days and the maximum consecutive days above those thresholds were also quantified to determine the exclusion temperature. Thresholds were analysed with 0·1 °C of resolution. The ability of these thresholds to forecast the presence/absence of trout was tested by means of Hanssen–Kuiper criterion (HK) (McBride and Ebert 2000). Ideally, HK requires the same positive and negative true scores, such that any deviation will influence the final value. Thus, we selected the highest relative value of HK to identify the best forecaster of the trout distribution boundary. We also calculated the BIAS (McBride and Ebert 2000), hit ratio (h.r.) and standard deviation (s.d.) to assess the selection.

Analysis of DMST, daily maximum stream temperature and their 7-day moving average supported the choice of threshold criteria (Appendix A).

Other niche traits

In addition to temperature, other constraints define the brown trout realized niche (e.g. Armstrong *et al.*, 2003). The predictive capacity of chemical, physical, hydrological and biological traits was analysed by means of three methods: *t*-test, generalized linear models (GLM, significance level: 0·1) and receiver operating characteristic curve (ROC). Then, these traits were compared against temperature variables (times above the threshold during 7 days or more, values of the model parameters for each fishing site) to rank their relative importance as predictors of the presence/absence of trout. The analysed variables were as follows: chemical components (oxygen, phosphorus, nitrogen, conductivity, pH), BMWP' quality index (Alba-Tercedor and Sánchez-Ortega 1988), substrate composition (classes' frequency), mean discharge of the previous month (hm^3), channel slope and width, and density of each one of the species of the fish community.

RESULTS

Trout presence

Brown trout were not detected downstream from C24 in the Cega stream or from P8 in the Pirón stream. Trout were

also absent in intermediate C14 and P3 sites in the first year, whereas in C15, only one trout was captured each year. In C24, one trout was caught in the first sampling, and six trout were caught in the second sampling. The catches at sampling sites downstream of C18 were not homogeneous between 1997 and 1998 because catches occurred in only one of the two sampling events in these sites, with the exception of C20. Although the Pirón stream is a tributary of the Cega stream, the trout populations of both streams are not connected to each other.

The altitudinal lower limits of the brown trout range were located at approximately 730 m a.s.l. in the Cega stream and at 820 m a.s.l. in the Pirón stream at the time of sampling.

Stream temperature

The thermographs recorded 544 days of data (with the exception of Ct4: 407 days, Ct6: 501 days, Pt2: 483 days and Pt5: 424 days) (Supporting Information S1). All the estimated parameters of the stream temperature models were significant ($p < 0{\cdot}025$), and the proposed modified model showed better values for AIC, RMSE and BIC than the Mohseni *et al.* (1998) model when DMST is used (Table III). The RMSE average for thermal samples ranged from 1·08 to 1·93 °C. Only the Pt2 (1335 m a.s.l.) and Pt3 (905 m a.s.l.) sites showed anomalous thermal behaviour, but the values were within the RMSE range. The Torrecaballeros dam is altering the natural thermal regime upstream of the Pt2 site (Santiago *et al.* 2013), which causes difficulty in modelling. Drainage by spillways of the heated water by solar radiation at the beginning of spring is postulated as responsible for fast increase in temperature of the water under the dam at that time. Snow-melting homogenized again the water temperature, after which the increasing temperature trend returns. When in the transition from spring to summer the water level descends, drainage is done by the bottom drainage and the outlet temperature decreases. Torrecaballeros reservoir is relatively small, and when water level drops at summer, hypolimnetic and epilimnetic water mixed and heated quickly. Then, water drainages by the bottom are very much warmer than if there was no reservoir. In addition, a spring and a catchment for drinking water produced an anomalous performance of thermal models near the Pt3 site by smoothing the expected temperature oscillations and altering the thermal flux in dependence on the quantity of abstracted water.

Thermal threshold determination

The brown trout thermal boundaries (1997–1998) were determined by the absence of trout and the occurrence of events of 7 or more consecutive days (henceforth c.d.) above 18·7 °C DMST in Cega (HK = 0·524, BIAS = 0·881, h.r. = 0·844, s.d. = 0·131) and above 18·1 °C in Pirón (HK = 0·857, BIAS = 1·071, h.r. = 0·952, s.d. = 0·045) at the time of sampling. The results of Pirón show a threshold band between 17·2 and 18·1 °C, but the latter was chosen because the stream temperature change ratio is insignificant above 17·2 °C at the border of the observed trout range; otherwise, the threshold could be underestimated. These observed thresholds are lower than the critical feeding temperature for this species (between 19·4 and 26·8 °C, in Elliott and Elliott 2010).

The number of days per year above the different thresholds (DAT), the number of times per year above the 7 or more c.d. threshold (TAT ≥ 7) and the maximum c.d. per year above the thresholds (MCDAT) are shown in Table IV.

Other niche traits

GLM analyses showed that 73–88% of the deviation of trout density (global and stratified by age classes) was explained by linear models using hydrological, substrate and temperature-related variables as predictors.

Table III. Akaike information criterion (AIC), root mean square error (RMSE) and Bayesian information criterion (BIC) values for daily mean stream temperature models with four and five parameters (Mohseni *et al.* 1998 model and modified model in this study, respectively).

	AIC		RMSE		BIC	
Thermograph	Four parameters	Five parameters	Four parameters	Five parameters	Four parameters	Five parameters
Ct1	1866·5	1794·8	1·914	1·292	1887·9	1820·5
Ct2	1935·9	1848·6	2·217	1·359	1957·3	1874·3
Ct3	2138·5	2084·3	3·508	1·695	2204·9	2109·9
Ct4	1436·3	1337·9	2·179	1·296	1456·2	1361·8
Ct5	1743·6	1605·7	1·544	1·082	1765·0	1631·4
Ct6	1920·9	1825·5	2·936	1·544	1941·9	1850·7
Pt1	1771·0	1701·4	1·611	1·184	1792·4	1727·1
Pt2	1988·2	1965·4	3·929	1·920	2009·0	1990·4
Pt3	1625·0	1606·4	1·221	1·083	1646·4	1632·1
Pt4	1768·1	1650·1	1·593	1·128	1789·5	1675·8
Pt5	1581·3	1092·0	2·428	1·267	1601·6	1114·8

Table IV. Number of days per year above the different thresholds (DAT), number of times per year above the thresholds during 7 or more consecutive days (TAT≥7) and the maximum number of consecutive days per year above the thresholds (MCDAT) in each location for the sampling years.

	DAT		TAT≥7		MCDAT	
Location	1997	1998	1997	1998	1997	1998
18·7 °C						
C1						
C2						
C3						
C4	1	10			1	6
C5	12	14	1	1	7	7
C6	20	25	2	1	10	8
C7	16	20	1	1	9	8
C8	10	14			3	6
C9	8	12			3	6
C10	1	11			1	6
C11	1	8			1	5
C12		4				4
C13						
C14						
C15						
C16						
C17						
C18		4				4
C19		7				5
C20	1	9			1	6
C21	1	11			1	6
C22	1	11			1	6
C23	5	12			3	6
C24	9	15			3	6
C25	16	16	1	1	9	7
18·1 °C						
P1						
P2						
P3						
P4						
P5						
P6						
P7						
P8						
P9	9	7	1	1	1	5
P10	13	22	3	1	10	7
P11	13	23	3	1	11	13
P12	13	23	3	1	13	22

Thresholds: 18·7 °C in Cega and 18·1 °C in Pirón.

Specifically, GLM model including community structure explained 17% of deviance (AIC 437·98) of the total density. Models using average flow of July, temperature variables and substrate explained 69% (AIC 379·09), 78% (AIC 367·34) and 81% (AIC 361·60), respectively. A GLM model containing all these potential predictors showed lower AIC scores (341·51, explained deviance: 86%) than models including only one type of variables. Similarly, 44% of deviance of 3++ trout density was explained by community structure (AIC 398·68) and 37% by temperature (AIC 407·07). GLM of age class 3++ with all types of variables yields 68% of explained deviance (AIC 382·80). Age class 3++ is the most abundant in the lower part of the trout distribution in these streams (Junta de Castilla y León, 1997) and was considered the best age class to be used for the threshold determinations.

Results of the ROC analysis showed that the only reliable predictor was TAT≥7. This predictor exhibited an area under the curve of 0·84; when density influence was studied instead of presence/absence, area under the curve was 1·0 (the best result). The density of other species was not as reliable.

Finally, the results of *t*-test (Bonferroni correction) are consistent with the results showing TAT≥7 as the only reliable predictor ($p = 1{\cdot}3e\text{-}5$).

Climate change

The observed thresholds (18·7 °C in Cega and 18·1 °C in Pirón) were studied for the climate change scenarios. The frequency of higher DMST than the observed thresholds increased with time in both scenarios. As expected, this frequency was significantly higher in RCP8·5 than in RCP4·5 (Figure 4). The frequency of longer intervals (7 or more days, Figure 5) of high temperatures increased in the same way, which reached a maximum of 56 c.d. in the C6, C7 and C25 sites at 18·7 °C in RCP8·5. In the P11 and P12 sites, the maximum was 59 c.d. at 18·1 °C in the same scenario (Figure 6).

The decadal average (period 2090–2099) of the DAT, TAT≥7 and MCDAT was modelled in each sampling site for each climate change scenario (Table V). The results at the Cega stream demonstrate that the DAT increased 4·0 times (average value) in RCP4·5 and 13·9 times in RCP8·5. The TAT≥7 increased 2·4 times in RCP4·5 and 2·9 times in RCP8·5. The MCDAT increased 3·0 times in RCP4·5 and 9·2 times in RCP8·5. At the Pirón stream, the average values were as follows: DAT, 5·6 times in RCP4·5 and 8·5 times in RCP8·5; TAT≥7, 1·8 times in RCP4·5 and 2·0 times in RCP8·5; MCDAT, 4·5 times in RCP4·5 and 7·3 times in RCP8·5.

The RCP4·5 scenario forecasts that 7 c.d. above the thresholds will occur at 785 m a.s.l. (Cega stream) and 830 m a.s.l. (Pirón stream); in the RCP8·5 scenario, these altitudes will be at 830 m a.s.l. and 831 m a.s.l., averaged over forecasts for the 2090–2099 period. A warm window in the intermediate reach characterized by the Ct3 site (1043 m a.s.l.) in Cega would also open as a consequence of climate change. In this sense, warmer waters could extend to 941 m a.s.l. (RCP4·5) or 913 m a.s.l. (RCP8·5) downstream. The upstream boundary of this window was associated with a water infiltration area beginning at approximately 1050 m a.s.l. and continuing downstream.

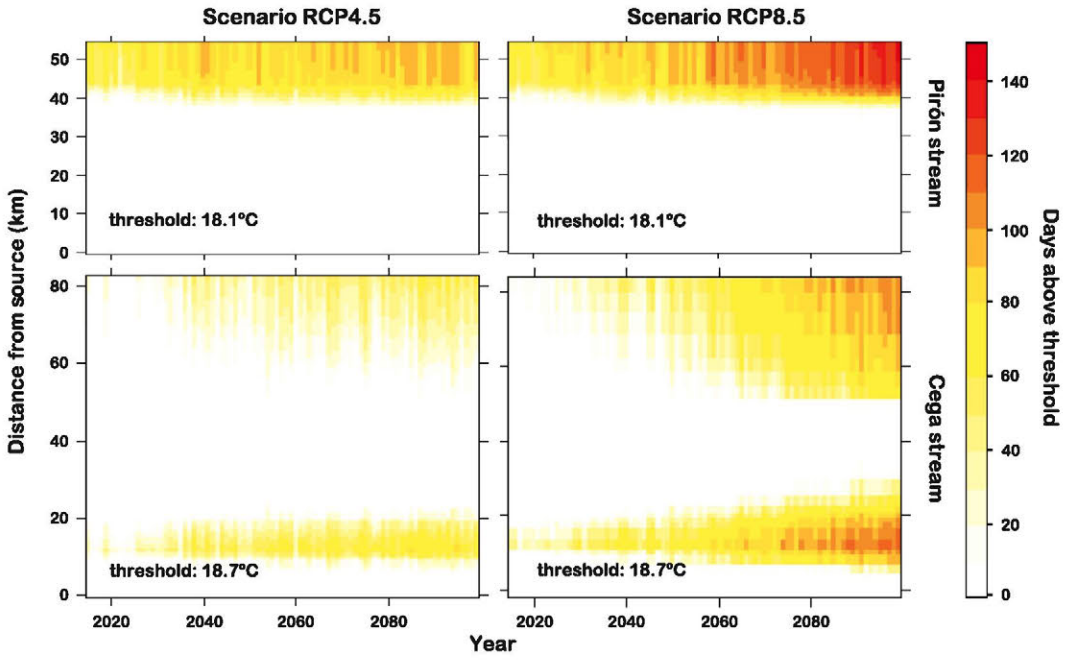

Figure 4. Forecast of the number of days above thermal thresholds up to the year 2099 along the fluvial continuum in the Cega and Pirón streams. Threshold: 18·7 and 18·1 °C in the Cega and Pirón streams, respectively. Scenarios for RCP 4·5 and 8·5 are shown. Graphic resolution: 1 km.

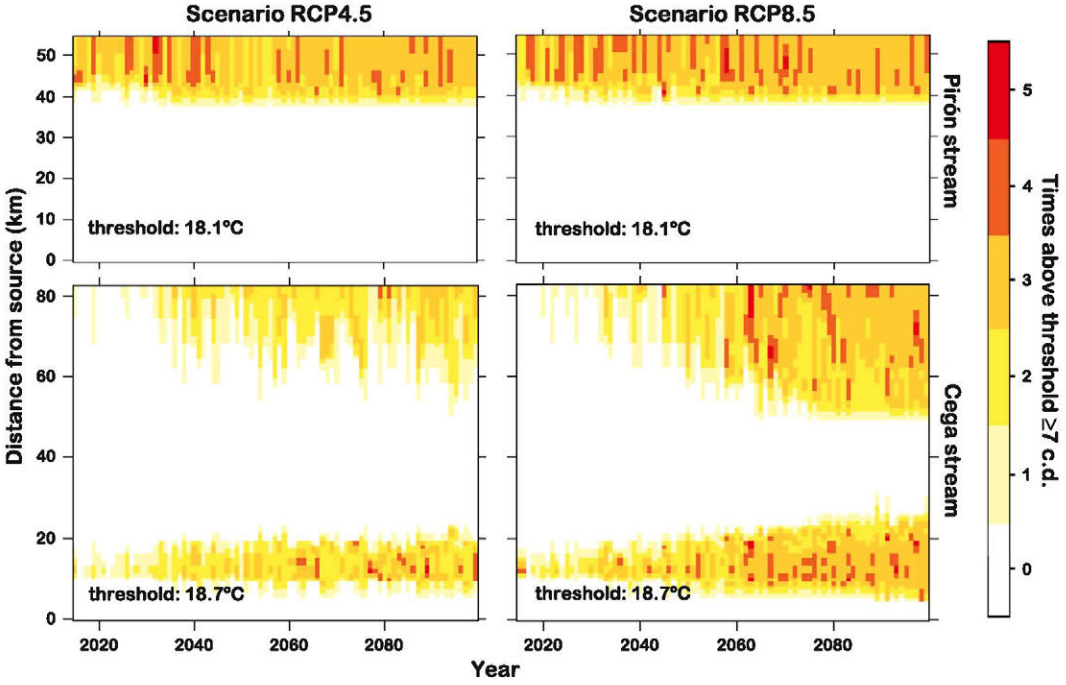

Figure 5. Forecast of the times that the thresholds exceeded 7 or more consecutive days (c.d.) up to the year 2099 along the fluvial continuum in the Cega and Pirón streams. Threshold: 18·7 and 18·1 °C in the Cega and Pirón streams, respectively. Scenarios RCP 4·5 and 8·5 are shown. Graphic resolution: 1 km.

DISCUSSION

Daily mean temperature models were accurate enough to be used in rebuilding and forecasting water temperatures from air temperatures. Thus, high reliability was possible for determining the thermal performance of Cega and Pirón streams. Differences between 1997 and 1998 flow regimes introduced a useful variability for the analysis. On the other hand, the high spatial density of data of fish populations and physical habitat variables allowed inferences to be reliable in spite of the relatively short time series data.

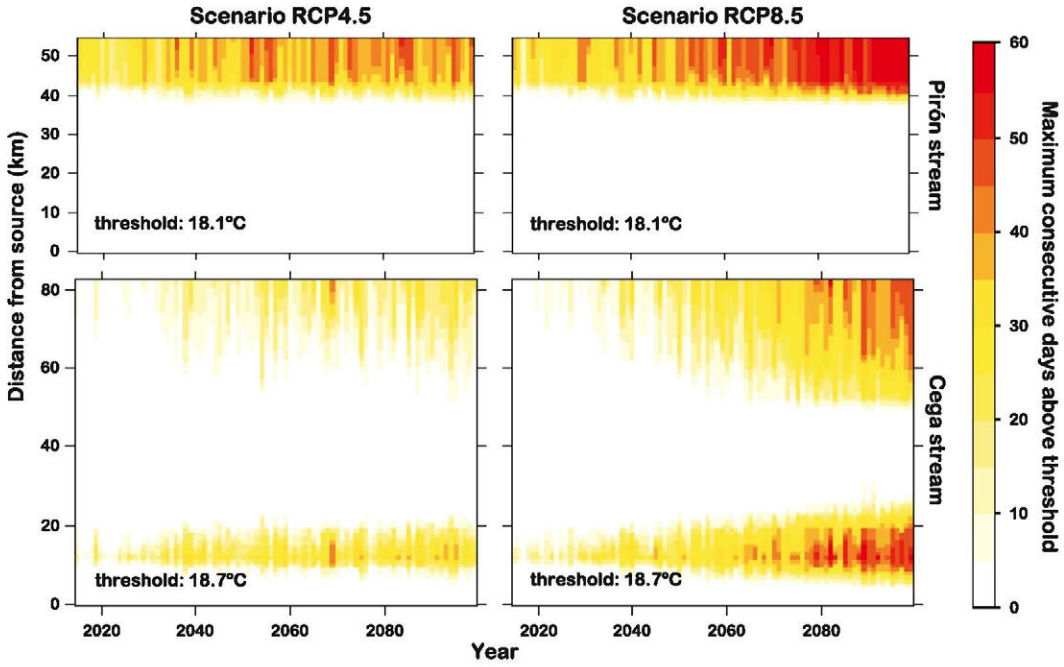

Figure 6. Forecast of the maximum number of consecutive days above thresholds up to the year 2099 along the fluvial continuum in the Cega and Pirón streams. Threshold: 18·7 and 18·1 °C in the Cega and Pirón streams, respectively. Scenarios RCP 4·5 and 8·5 are shown. Graphic resolution: 1 km.

The temperature threshold of presence/absence can be influenced by the community composition, reducing the thermal realized niche of trout in these streams. It is known that brown trout and Arctic char (*Salvelinus alpinus*) share spatial and trophic niches coexisting or excluding each other in function of other environmental characteristics (system productivity, temperature – Finstad *et al.* 2011). The combination of temperature and competition to determine distribution is also known in other ectothermic groups, as lizards (Buckley and Roughgarden, 2006). The River Cega basin populations are living in the southern edge of the brown trout distribution, and they share the space with cyprinids (Iberian barbel *Luciobarbus bocagei*, Northern Iberian chub *Squalius carolitertii*) that may compete with it for space and trophic resources in the lower reaches, where cyprinids are more efficient than trout. Sánchez-Hernández and Cobo (2011) found important diet overlap values in sympatry between these species. These authors suggest that 'differences in macrohabitat use, drift behaviour of prey and prey size are important adaptive features that may reduce the inter-specific competition in the fish community and permit the food partitioning that allows coexistence'. Nonetheless, community structure is long known as a determinant of the species abundance (e.g. Tokeshi, 1993). Other environmental variables (hydraulics, temperature) also influence the density of fish populations (Ayllón *et al.* 2013).

The study of habitat variables showed that temperature (TAT ≥ 7 days) was the most reliable predictor for trout presence/absence. In agreement with this, the observed limits of the summer distribution of brown trout were linked to DMST thresholds between 18·1 and 18·7 °C. These limits were lower than the critical feeding temperature for brown trout as given by Elliott *et al.* (1995) (19·4 °C) and Forseth *et al.* (2009) (at least 23 °C), as well as the upper critical temperature range (20–30 °C, ultimate lethal temperature: 29·7 °C/10 min, in Elliott 2000) and the incipient lethal temperature (24·7 °C up to 7 days, Elliott 1981). The upper thermal limit found by Hari *et al.* (2006) using sinusoidal regression was 20·0 °C. Competitive interactions are known to influence the realized niche thresholds (Finstad *et al.* 2011; Fey and Herren, 2014). Thus, relatively high temperatures may be related to long periods of physiological inefficiency, which make trout less competitive for space and may favour its exclusion from warmer sites. However, the observed limits may be influenced by other constraints such as low summer flow, which could reduce the suitable habitat (Wenger *et al.* 2011). In this sense, we observed very low flow downstream of the P5 site (879 m a.s.l.) in the Pirón stream in summer. Water quality was discarded as a significant driver of the distribution as there are no significant differences in either physical–chemical parameters or the index value BMWP' (Alba-Tercedor and Sánchez-Ortega 1988) between sampling sites with and without trout (Junta de Castilla y León, 1997).

Moreover, we estimated high summer temperatures (up to 20 °C but less than 7 c.d.) in the piedmont zone, coinciding with karst geology, which supports a healthy trout population. Subsurface infiltration occurs in the karst

Table V. Decadal average (2090–2099) of the number of days per year above the different thresholds (DAT), number of times per year above the thresholds during 7 or more consecutive days (TAT ≥ 7) and the maximum number of consecutive days per year above the thresholds (MCDAT) modelled in each survey location.

	DAT		TAT ≥ 7		MCDAT	
Location	RCP4·5	RCP8·5	RCP4·5	RCP8·5	RCP4·5	RCP8·5
18·7 °C						
C1						
C2		0·1				0·1
C3	0·3	33·4		1·4	0·3	10·6
C4	30·0	87·8	1·6	2·9	14·4	40·5
C5	49·0	97·8	2·6	3	21·8	44·8
C6	69·3	108·0	2·6	3·3	30·8	49·7
C7	60·1	103·4	2·5	3·2	28·8	45·7
C8	46·0	96·2	2·3	3·1	18·2	43·7
C9	41·7	93·6	2	3·1	17·1	41·3
C10	25·6	84·1	1	3	10	34·1
C11	15·2	75·0	0·6	2·5	5·2	29·8
C12	5·3	58·0		2·2	1·9	17·6
C13	0·8	30·7		0·2		5·5
C14	0·1	5·9			0·1	1·4
C15		0·1				0·1
C16						
C17		0·1				0·1
C18	8·3	67·1	0·1	2·6	3·2	25·6
C19	12·2	73·4	0·4	2·7	4·4	29·7
C20	20·9	81·7	0·9	2·6	8·2	33·7
C21	27·9	86·4	1·2	3·2	11·2	36·5
C22	29·6	87·0	1·5	3	11·9	38
C23	40·4	94·0	2·1	3·2	16·9	41·8
C24	47·3	97·0	2·3	3	20·4	44·5
C25	52·9	99·1	2·7	3·1	23	44·8
18·1 °C						
P1						
P2						
P3						
P4						
P5						
P6						
P7						
P8	0·1	5·5				
P9	58·9	101·4	2·5	3	23·3	43·5
P10	85·8	123·6	3·2	3·2	37·9	56
P11	89·3	128·2	3·2	3·2	39·2	56·7
P12	90·2	129·8	3·1	3·2	40·7	57·4

Thresholds: 18·7 °C in Cega and 18·1 °C in Pirón. Climate change scenarios: RCP4·5 and RCP8·5 (Taylor *et al.* 2009).

reach, and the flow loss favours further warming of the Cega stream. Moreover, infiltration and water discharge occur at different locations to and from the underlying aquifer, particularly downstream of the Ct3 and Ct4 sites. The groundwater discharge provides resistance to thermal change forced by the atmosphere–water energy balance (O'Driscoll and DeWalle 2006), but the discharge temperature can also be affected by global warming (Kurylyk *et al.* 2013). At the headwaters of these streams, trout can tolerate very low temperatures under the lower growth threshold (Borgstrøm and Museth, 2005, Elliott and Elliott 2010), possibly because competition with other species and hypoxic stress do not exist.

On the basis of climate change forecasts, the thermal habitat is expected to induce the mentioned retractions of the brown trout range by the year 2100. In the Cega stream, this reduction would affect 24% and 38% of the stream length occupied by brown trout, as estimated from 1997 and 1998 sampling events for the RCP4·5 and RCP8·5 scenarios, respectively. Differences among communities at lower and middle Cega reaches may induce differences in the threshold behaviour, and thus, the thermal window detected in the piedmont zone could cause additional losses of 11% and 18% in habitat length for the RCP4·5 and RCP8·5 scenarios. The Pirón stream reduction would affect 8% and 11% of the habitat length for the RCP4·5 and RCP8·5 scenarios, respectively; thus, relevant differences between scenarios do not exist. This may be because the stream thermal regime upstream of the P8 site is influenced by groundwater discharges, and thus, the effects of extreme summer temperatures are lessened. Moreover, other stressors such as low flow could contribute to the lower observed temperature threshold at the Pirón stream than at the Cega stream, thereby lessening the apparent effects of warming in the Pirón stream compared with the Cega stream.

Predicted thermal habitat losses are important but not as dramatic as the forecasts of other studies at higher latitudes in the Iberian Peninsula (almost the entire stream length in Almodóvar *et al.* 2011; 57% of reaches in Filipe *et al.* 2013). We forecast a thermal habitat loss of up to 38% (56% with warm window), despite using a more unfavourable scenario for CO_2 emissions (RCP8·5) in our study (Rogelj *et al.* 2012). The differences in our study compared with those of other authors may be because we worked at a finer scale (more spatially intensive data) and used more recent climate models and more direct methods for downscaling and modelling stream temperature. Moreover, most of the reviewed papers used the weekly mean of the maximum temperature (i.e. Webb and Walsh 2004; Almodóvar *et al.* 2011; Roberts *et al.* 2013); we found that the use of the weekly mean added inaccuracy to the threshold study. In addition, we used daily mean temperature instead of the maximum temperature because the mean is more representative of the average conditions.

The expected high summer temperatures might disconnect the population at the middle reaches of the Cega stream by the occurrence of the warm window. This fragmentation would exacerbate the predicted decrease in the trout population of this stream. The cumulative effects of climate change and other human impacts can aggravate the negative effects on salmonids (Walters *et al.* 2013). Combined flow reduction and temperature increase can exacerbate the reduction of cold-water habitat (Arismendi

et al., 2012). Water abstractions and extractions (water wells) for irrigation are particularly important in the Cega and Pirón basins. If the current use of water remains stable or increases and if forecasted precipitation reductions (IPCC 2013 and our unpublished analysis) are fulfilled, the habitat reduction of brown trout may become critical. A large number of species may have their distribution range altered; fish are particularly sensitive because connectivity between suitable areas is difficult (Abell *et al.* 2008). The biogeographical implications of global warming could be particularly dramatic in the Mediterranean area due to the synergistic effects of warming and flow reduction.

Additional research on the effects of climate change on freshwater fishes must be performed; however, care must be taken not to confuse the fundamental and realized niches (Pearson and Dawson 2003). Physiology can dictate the limits of fish tolerance, but these limits can be more constrained by additional biotic and abiotic restrictions, such as competition (biotic) or hydromorphology (abiotic). Trout show relative thermal plasticity at early stages of development, and this may promote adaptation if the changes are not sudden in the adaptive sense (Jensen *et al.* 2008); however, this plasticity is limited. Warmer events could possibly be tolerated; however, the trout realized niche appears to be narrower than the physiological limitations.

Our methodological approach is also an outcome of this study. The methodology used in this study allowed a noticeable increase in the reliability and the spatial–temporal accuracy of the forecasts, as well as a reduction in uncertainty. Downscaling is sometimes referred to as the direct interpolation of original coarse grids from climate models to points of interest. In other cases, downscaling uses grids constructed from observed data and not local observations. Both of these downscaling techniques depend too heavily on the characteristics of the interpolation technique and the density of meteorological stations, which do not take into account the local climate. We therefore preferred the complete downscaling of several climate models at our selected meteorological station. The downscaling method and the systematic error correction provide low-error results, and these methods are readily applicable to similar studies that need absolute values of the expected future changes. Likewise, the use of the latest scenarios established for climate change studies represents an update of previous forecasts.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.

APPENDIX A: DETERMINATION OF THE SUITABLE TIME SCALE AND UNITS FOR STUDYING THRESHOLDS

Objectives

The suitability of using daily mean stream temperature (DM), 7-day moving average of DM, daily maximum stream temperature (DMax) and 7-day moving average of DMax to model thermal behaviour of streams and to determine the brown trout presence/absence thresholds for brown trout was contrasted.

Methods

The studied models were as follows:

- The logistic model proposed in this paper was used with daily data (mean and maximum values).
- Mohseni *et al.* (1998) logistic model was used with 7-day moving average data (mean and maximum values).
- A linear model was used with 7-day moving average of daily maximum summer temperatures (June to September).

Root mean square error (RMSE) was used as an indicator of the reliability of models (mean, maximum and minimum values).

Thermal thresholds were calculated from the aforementioned models. Daily mean and maximum values were studied in events of 7 consecutive days. The rationale of these choices was described in the Materials and Methods section in the body (Stream Temperature Modelling and Thermal Threshold Determination sections).

Results and discussion

The results are shown in Tables AI and AII.

The models constructed with DM stream temperature (both the events of 7 consecutive days and the 7-day moving average) were more robust because they have lower RMSE, as with maximum and minimum values.

With respect to the calculation of thresholds, the more robust indicator with the Cega stream data was DM stream temperature in events of 7 consecutive days. With the Pirón stream data, HK, BIAS, h.r. and s.d. showed identical values, although the defined thresholds were not one value but a band of values. The narrowest band was obtained from DM stream temperature (again both the events of 7 consecutive days and the 7-day moving average). At the same time, these results were more similar to each other than those obtained from DMax.

Table AI. Average, maximum and minimum root mean square error for each model.

	Root mean square error (°C)				
	Daily mean (modified logistic model)	Daily mean 7-day moving average (logistic model)	Daily maximum (modified logistic model)	Daily maximum 7-day moving average (logistic model)	Daily maximum 7-day moving average (linear model)
Average	1·35	1·16	1·76	1·50	1·38
Maximum	1·92	1·82	2·27	1·92	4·69
Minimum	1·08	0·88	1·32	1·05	0·24

Table AII. Estimated thresholds and their values for Hanssen–Kuiper (HK), BIAS, hit ratio (*h.r.*) and its standard deviation (*s.d.*) (McBride and Ebert, 2000).

	Threshold determination				
	Daily mean (7 consecutive days)	Daily mean 7-day moving average	Daily maximum (7 consecutive days)	Daily maximum 7-day moving average (logistic model)	Daily maximum 7-day moving average (linear model)
Cega stream					
Threshold	**18·7 °C**	**19·5 °C**	**19·7 °C**	**21·0 °C**	**19·2 °C**
HK	0·55	0·32	0·44	0·34	0·22
BIAS	0·90	0·37	0·44	0·34	0·22
h.r.	0·86	0·36	0·48	0·39	0·27
s.d.	0·12	0·23	0·25	0·24	0·20
Pirón stream					
Threshold	17·2–**18·1** °C	17·5–**18·3** °C	18·1–**19·5** °C	19·0–**20·6** °C	18·6–**19·9** °C
HK	0·86	0·86	0·86	0·86	0·86
BIAS	1·07	1·07	1·07	1·07	1·07
h.r.	0·95	0·95	0·95	0·95	0·95
s.d.	0·05	0·05	0·05	0·05	0·05

Bold letters indicate the chosen thresholds for each model.

The upper values of the bands were chosen as thresholds because the stream temperature change ratio is insignificant above the lower value of the threshold ranges at the border of the observed trout distribution; otherwise, the threshold could be underestimated.

A thermal anomaly (a 'warm window' associated with a water infiltration area in which the gravels and boulders of the streambed are especially heated in summer by solar radiation) in an intermediate reach of the Cega stream prevented values for HK, BIAS and h.r. from being as good as those obtained from the Pirón stream data.

Conclusions

For the objectives of this paper, DM was the best solution to model thermal behaviour of the streams, and the study of events of 7 consecutive days above the threshold was better than 7-day moving average. Thus, the arguments given in the methodological description of the main body of this paper are reinforced.