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Predicting shifts in the climate space of freshwater fishes in Great Britain due to climate change

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ABSTRACT

The implications of climate change for terrestrial and aquatic taxa are for their dispersal pole-wards and/ or to higher altitudes as they track their climate niches. Here, bioclimatic models are developed to predict how projected climate change scenarios for a northern temperate region (Great Britain) shift the climate spaces (i.e. areas of suitable thermal habitat) for 12 freshwater fishes of the Salmonidae, Percidae, Esocidae and Cyprinidae families. Climate envelope models developed in Biomod2 used the current species' distributions and their relationships with current climatic variables, and projected these onto the BCC-CSM1-1 and HadGEM2-AO climate change scenarios (low and high emissions, 2050 and 2070) in full and no dispersal scenarios. Substantial contractions in climate spaces were predicted for native salmonid fishes, with decreases of up to 78% for Atlantic salmon *Salmo salar*, with these largely unchanged between the dispersal scenarios. Conversely, for the majority of cyprinid fishes, expansions were predicted, including into northern regions where they are current not present biogeographically. Only under the no dispersal scenarios did their predicted distributions remain the same as their current distributions. For all non-salmonid species, the most important climate variables in the model predictions related to temperature; for salmonids, they were a combination of temperature and shifts in annual mean precipitation. As these predictions suggest that there is potential for considerable alterations to the climate spaces of freshwater fishes in Great Britain during this century then regulatory and mitigation conservation actions should be undertaken to minimise these.

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1. Introduction

Freshwater environments and their fishes are especially sensitive to the effects of climate change as the persistence and quality of aquatic habitats are strongly reliant on climatic and hydrologic regimes (Morrongiello et al., 2011). The vulnerability of freshwater fish communities to altered climatic patterns is highlighted by their isolation and fragmentation within terrestrial landscapes that typically result in river basins acting as biogeographic islands (Fausch et al., 2002; Gozlan et al., 2010; Olden et al., 2011). This reliance on climate patterns for their thermal regimes and hydrology suggest that they will be particularly vulnerable to changes that result from the alterations in air temperatures and precipitation patterns that are projected to occur during this century (Johnson et al., 2009; Hobday and Lough, 2011).

The predicted effects of climate change on fishes are associated with their thermal tolerances (Rahel and Olden, 2008); where these are due to be either surpassed or optimised for species due to warming then range shifts and expansions can be expected (Graham and Harrod, 2009; Morrongiello et al., 2011; Comte and Grenouillet, 2013, Comte et al., 2013). The species-specific effects of temperature changes on

distributions of freshwater fishes are a reflection of the interactions of their changing hydrological and thermal habitats with their physiological and life-history characteristics, and thus potentially result in considerable effects at the species level that will then affect patterns of freshwater biogeography at larger spatial scales (Heino et al., 2009). In general, climate change predictions for both terrestrial and aquatic taxa tend to be for movements pole-wards and/or to higher altitudes (Chen et al., 2011; Comte and Grenouillet, 2013; Holding et al., 2015), as species attempt to track their climate niches (Crimmins et al., 2011).

In predicting how climate change will alter the distribution of species, bioclimatic envelopes assess the responses of a species to current climatic conditions in order to predict how their distribution will then alter in projected future climate scenarios (Berry et al., 2002; Heikkinen et al., 2006). Bioclimatic envelopes assume that climate is the primary factor determining species' distributions, and that range shifts will occur promptly in response to climate change (Woodward and Beerling, 1997; Hampe, 2004). For freshwater fishes to track their climate niche then they must either be able to disperse through suitable corridors that connect their isolated habitats (Poff et al., 2002) or they will require some managed translocations, a continuing source of debate (e.g. Olden et al., 2010, 2011; Schwartz et al., 2012). Thus, the utility of bioclimatic models for the conservation management of freshwater fishes is arguably their identification of how the areas of

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suitable thermal habitat available to species (hereafter referred to as their climate space) will alter, highlighting the species and spatial areas of their existing ranges that are most vulnerable to the adverse effects of climate change (Staudt et al., 2013). The identification of the fishes and basins at most risk of alterations in their distribution of their species can then be prioritised for immediate management actions that should then provide the greatest long-term conservation benefits.

The aim of this study was thus to develop bioclimate models to predict how climate change could alter the available climate space for a range of freshwater fishes across a number of families with varying thermal preferences in a northern temperate region during this century (2050 and 2070). The model region was Great Britain, which has sufficient latitude, longitudinal and altitudinal ranges to provide marked differences in regional climates, and the model fishes were 12 species from across four families of varying thermal tolerances and with strong data on their presence/absence. It was predicted that the available climate space for each fish species would shift northwards under the modelled climate change scenarios, but the extent of the changes would vary at both species and family levels.

2. Materials and methods

The modelled fishes were from the families Salmonidae (*Salmo trutta*, *Salmo salar*), Percidae (*Perca fluviatilis*), Esocidae (*Esox lucius*) and Cyprinidae (*Cyprinus carpio*, *Carassius carassius*, *Scardinius erythrophthalmus*, *Rutilus rutilus*, *Squalius cephalus*, *Abramis brama*, *Leuciscus leuciscus* and *Gobio gobio*). For the latter five species of the Cyprinidae family, data were reported initially in Ruiz-Navarro et al. (2016). However, their model predictions are included here in order to provide comprehensive comparisons across the four fish families and to present some new results from the models. Where the data from in Ruiz-Navarro et al. (2016) for these five cyprinid fishes are used in the Results, this original source has been cited appropriately.

As the 12 fishes were selected on the basis of their conservation, recreational and/ or socio-economic importance, this meant that species without these interests, such as minnow *Phoxinus phoxinus* and stone loach *Barbatula barbatula*, were not modelled. The modelled fishes included species with preferences for relatively cold waters (<15 °C, e.g. *S. salar*, *S. trutta*), cool waters (≤20 °C, e.g. *R. rutilus*, *S. erythrophthalmus*) and relatively warm waters (>20 °C, e.g. *C. carpio*) (Rahel and Olden, 2008; www.Fishbase.org). Other than *C. carpio*, all of the modelled species have native ranges in Great Britain. Due to their non-native status, *C. carpio* would normally not be suitable for climate modelling using the methodology outlined below, as they do not have a natural biogeographic range in Great Britain. However, their introduction history means they are considered naturalised in parts of Britain (primarily England) and have attained a widespread distribution during the last 100 years that suggests they are now present in all regions that are climatically suitable for their persistence (Britton et al., 2010).

Within the bioclimate models, data on the occurrences of the fishes within Great Britain were obtained from the 'Database for the Atlas of Freshwater Fishes', provided by the Biological Records Centre, available at the NBN Gateway website (https://data.nbn.org.uk/Datasets/GA000174). The majority of the records ranged from 1950 to 2003 in the British National Grid spatial reference system (based on the 1936 Ordnance Survey Great Britain datum, OSGB_36) at a 10 × 10 km resolution. They represent an accumulation of the recordings of each species over time within these grid squares and so all of the data were utilised in the models. The British National Grid spatial references were then converted to the World Geodetic System WGS_84 grid system so that the occurrence data matched the available climatic data. Species absences were considered to be sampled locations in Great Britain where fish species other than the fishes were present in the 'Database for the Atlas of Freshwater Fishes', i.e. squares that have not been visited by fish recorders were not considered for use in the modelling (Ruiz-Navarro et al., 2016).

The climate data utilised baseline (1950–2000) and future global projections of climate data (annual values) obtained from the WorldClim website (http://www.worldclim.org/, Hijmans et al., 2005), version 1.4 (release 3), at a 5-min resolution in the WGS_84 grid system. Climate projections for the years 2050 and 2070, under low (rcp 2.6) and high (rcp 8.5) emission scenarios were obtained from two different climate prediction models: BCC-CSM1-1 and HadGEM2-AO. BCC-CSM1-1 was produced by the Beijing Climate Center, China Meteorological Administration, whereas the Hadley Centre of the Meteorological Office of the UK produced HadGEM2-AO. The use of projections from both climate models thus provides 8 climate change scenarios for application to the bioclimate models and so a wider range of modelled scenarios than if only one climate model was used.

A 'UK outline polygon', obtained from the OS Opendata website (https://www.ordnancesurvey.co.uk/opendatadownload/products.html), was used to clip the climatic data to the area of Great Britain. The 19 climatic variables available, derived from the monthly temperature and rainfall values, were reduced to six through analysis of their correlations so that only variables with low pairwise correlations were used in the models (Dormann et al., 2013). This was completed through use of Pearson's correlation coefficient, with a threshold of $r = 0.70$ used to remove highly correlated variables from the climate data set (Ruiz-Navarro et al., 2016). As a result, the climatic variables used were: annual mean temperature (°C), mean diurnal range of temperature (°C), isothermality (100 ∗ (mean diurnal range / annual range of temperature)), mean temperature of wettest quarter (°C), mean temperature of driest quarter (°C), and annual precipitation (mm). The rationale for retaining these variables rather than their correlates was because they represent the two primary properties of the climate, energy and water that tend to be physiologically limiting factors for aspects of the biology and ecology of ectotherms, such as fish (Chu et al., 2005). It is, however, acknowledged that these climate variables are not the only determinants of fish distribution (Pont et al., 2006), with a range of other abiotic and biotic variables also often being important parameters that it was not possible to model here (Ruiz-Navarro et al., 2016).

Fish species distributions in Great Britain were modelled using seven algorithms available in the *biomod2* package (Thuiller et al., 2014) in R: (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) multivariate adaptive regression splines (MARS), (4) classification tree analysis (CTA), (5) boosted regression trees (BRT), (6) random forests (RF), and (7) artificial neural networks. In all models, the default options of *biomod2* were selected, with the exception of restricting the GAM smoothing to 4 knots to avoid over-fitting the data. Evaluation of the models was through the area under the ROC curve (AUC), using an 80:20 split of training to test data and 50 evaluation repetitions. AUC values range between 0 and 1, where 1 indicates excellent model performance and values lower than 0.5 indicate predictive discrimination that is no better than a random guess (Ruiz-Navarro et al., 2016). Marmion et al. (2009) outlined that the usefulness and accuracy of bioclimate models for conservation, i.e. their robustness, were improved when 'consensus' models were used, i.e. ensemble models. This was because ensemble models overcome the variability of predictions that can occur between single models. Thus, ensemble models were created in *biomod2* by weighting the single models by their AUC score, with only single models that had individual AUC evaluation scores of ≥0.7 included in the calculation. Where a single model had an AUC evaluation score below this then it would be excluded from the ensemble.

For the ensemble model of each species, the importance of the included climate predictors (i.e. annual mean temperature, mean diurnal range of temperature, isothermality, mean temperature of wettest quarter, mean temperature of driest quarter and annual precipitation) were then determined using the variables importance function, with the importance values converted to proportions (%) to facilitate their interpretation. These were run 10 times per species, with their mean (±SE) calculated.

Once the probability of presence of each species had been estimated for each geographic grid square by the ensemble models, a threshold of probability of presence was then applied to the cells. There are a number of options for selecting this threshold, including use of the threshold probability that maximises kappa and thus minimises prediction error based on current climate conditions (e.g. Huntley et al., 2008). However, models that have high probability thresholds (e.g. 0.8) tend to less good at generalising than models of low probability thresholds (e.g. 0.5), although use of the latter increases the chance of prediction error (Liu et al., 2011). Consequently, whilst thresholds of 0.5, 0.6 and 0.8 were tested initially, a threshold of 0.6 was selected for final use. The decision to use 0.6 across all models and species was based on the trade-offs between model generality and prediction error (Liu et al., 2005; Ruiz-Navarro et al., 2016).

Following the application of this threshold of probability of presence, the number of grid squares that were predicted to be occupied by each species was then counted for the different scenarios, and the location of the corresponding centroids was calculated. The ensemble models were then evaluated using the ROC curve (AUC), which is used extensively in species distribution modelling (SDM) (Elith et al., 2006), and it is generally considered the best metric for comparisons in the same geographic space (Buisson et al., 2008). The centroids of the simulated present ranges and the predicted future climate spaces of each species in each climate change projection were then calculated as the points about which the sum of the distances of all the grid squares in which the species was predicted to be present was zero, with the Euclidean distances from all cells to the centroid calculated and then tested for differences from the predicted centroid under the current conditions.

The model outputs were then compared between the different predictions under scenarios. The first was maximum dispersal, achieved in the model by enabling the predictions for each species to be projected across all of Great Britain. Thus, this represented a scenario where the species were free to move within Britain and thus track their climate niche fully. It was calculated as all of the squares in the new predicted range. The second was no dispersal of each species, achieved in the model by restricting predictions to the current range. Thus, this represented a scenario where each species was unable to move from its current distribution. It was calculated as the number of squares in the new predicted range that overlapped with the original predicted range. The modelling architecture did not allow for any other dispersal scenarios, for example, dispersal opportunities within and between catchments. The maximum dispersal scenario thus acknowledges that whilst the climate space of the species might be predicted to alter with a changing climate, this does not necessarily mean this will occur due to extant dispersal opportunities. Consequently, the outputs from the distribution-climate modelling of the fishes for each climate change projection was the simulated extent of the spatial area of Great Britain that populations of these fishes in current climate conditions (see Online Appendices 1,2), their distribution under minimum and maximum dispersal scenarios, and the climate variables contributing most to the predictions.

3. Results

The ensemble models predicting the distributions of the fishes included all of the individual models that were initially considered, as their AUC values were higher than 0.7 in all cases. All ensemble models had AUC values of ≥0.91 and, with the exception of S. trutta (0.49) had kappa values ≥0.64 (Table 1). The highest root mean squared error value was 0.44 (P. fluviatilis; Table 1).

The ensemble models predicted that the climate space of the two salmonid fishes in Great Britain would constrict under all projected climate change scenarios, with predicted declines of up to 56% for S. trutta and 78% for S. salar (Table 2; Fig. 1; Online Appendices 1,2). This shift in their climate space, as revealed by the direction and distance of centroid displacement, was displacement in a north-westerly direction of between 130 and 243 km for S. trutta and 78 to 293 km for S. salar

Table 1
Number of 10 × 10 km squares currently occupied in Great Britain by each species and the performance metrics of the ensemble distribution models per species. Area under the curve (AUC), Cohen's kappa coefficient (Kappa) and root mean squared error (RMSE).

Family	Species	Current squares	AUC	Kappa	RMSE
Salmonidae	S. trutta	2435	0.923	0.487	0.295
	S. salar	1503	0.917	0.671	0.408
Percidae	P. fluviatilis	1121	0.907	0.637	0.439
Esocidae	E. lucius	1066	0.905	0.650	0.429
Cyprinidae	C. carassius	174	0.927	0.619	0.356
	S. erythrophthalmus	547	0.925	0.657	0.388
	R. rutilus[a]	1073	0.954	0.758	0.348
	S. cephalus[a]	801	0.947	0.703	0.373
	A. brama[a]	796	0.944	0.706	0.357
	L. leuciscus[a]	785	0.945	0.697	0.373
	G. gobio[a]	894	0.942	0.700	0.363
	C. carpio	909	0.933	0.676	0.377

[a] Data presented in Ruiz-Navarro et al. (2016).

(Table 3; Fig. 2). The largest displacements were under the high emission scenarios of the HadGEM2-AO predictions. If there were no opportunities for the species to disperse from their current distribution, then considerable declines in their current distribution were predicted, particularly in the high emission scenario of HadGEM2-AO in 2070 (−56% for S. trutta and −83% for S. salar) (Table 4). However, even if these fishes have the opportunity to disperse to rivers where they are not currently present, the extent of their distribution decline will still be similar to no dispersal due to their current wide spatial distribution (Table 4). These two fishes were the only species where annual mean precipitation was an important variable contributing to the model predictions, with it being the most important variable for S. trutta (Table 5). For S. salar, the most important predictor was annual mean temperature (49.9%; Table 5).

The climate spaces of P. fluviatilis and E. lucius in Great Britain were predicted to expand, with increases of between 35 and 62%, and 37 and 67% respectively (Table 2; Online Appendices 1,2). Whilst the shifts in these distributions were also predicted to be in a north-westerly direction, these were comparatively low when compared with the salmonids, with predicted shifts of between 40 and 78 km for P. fluviatilis and

Table 2
Grade of change (%) in the number of squares occupied by the species for each projected future scenario. Low ES: low emissions scenario; High ES: high emissions scenario. (See Online Appendix 1 for full table including changes in the numbers of occupied squares).

|	Year	BCC-CSM1-1 Low ES	BCC-CSM1-1 High ES	HadGEM2-AO Low ES	HadGEM2-AO High ES	Source
S. trutta	2050	−32.20	−41.31	−35.81	−40.83	This study
	2070	−30.31	−56.27	−29.34	−53.15	
S. salar	2050	−42.33	−58.35	−52.20	−65.92	This study
	2070	−47.67	−71.60	−44.69	−78.09	
P. fluviatilis	2050	35.13	48.66	61.53	65.69	This study
	2070	38.30	48.17	58.35	72.62	
E. lucius	2050	37.01	49.23	67.09	66.50	This study
	2070	38.38	49.23	60.85	75.73	
C. carassius	2050	-28.57	65.80	123.81	184.20	This study
	2070	-43.51	45.24	119.26	294.59	
S. erythrophthalmus	2050	76.78	122.81	119.54	134.15	This study
	2070	84.15	130.74	108.61	177.60	
R. rutilus	2050	44.45	58.23	67.42	73.31	Ruiz-Navarro et al. (2016)
	2070	46.71	58.75	63.26	84.23	
S. cephalus	2050	−42.20	−72.25	−18.54	−38.75	Ruiz-Navarro et al. (2016)
	2070	−19.82	−82.23	−2.30	−77.75	
A. brama	2050	79.93	106.94	108.18	124.41	Ruiz-Navarro et al. (2016)
	2070	89.10	113.88	95.91	143.37	
L. leuciscus	2050	6.33	−9.61	−18.52	−30.13	Ruiz-Navarro et al. (2016)
	2070	15.59	−46.66	6.10	−88.39	
G. gobio	2050	−4.19	−54.07	−18.33	−44.68	Ruiz-Navarro et al. (2016)
	2070	24.89	−64.48	11.43	−91.40	
C. carpio	2050	67.74	100.24	101.79	118.93	This study
	2070	77.62	102.74	87.26	135.60	
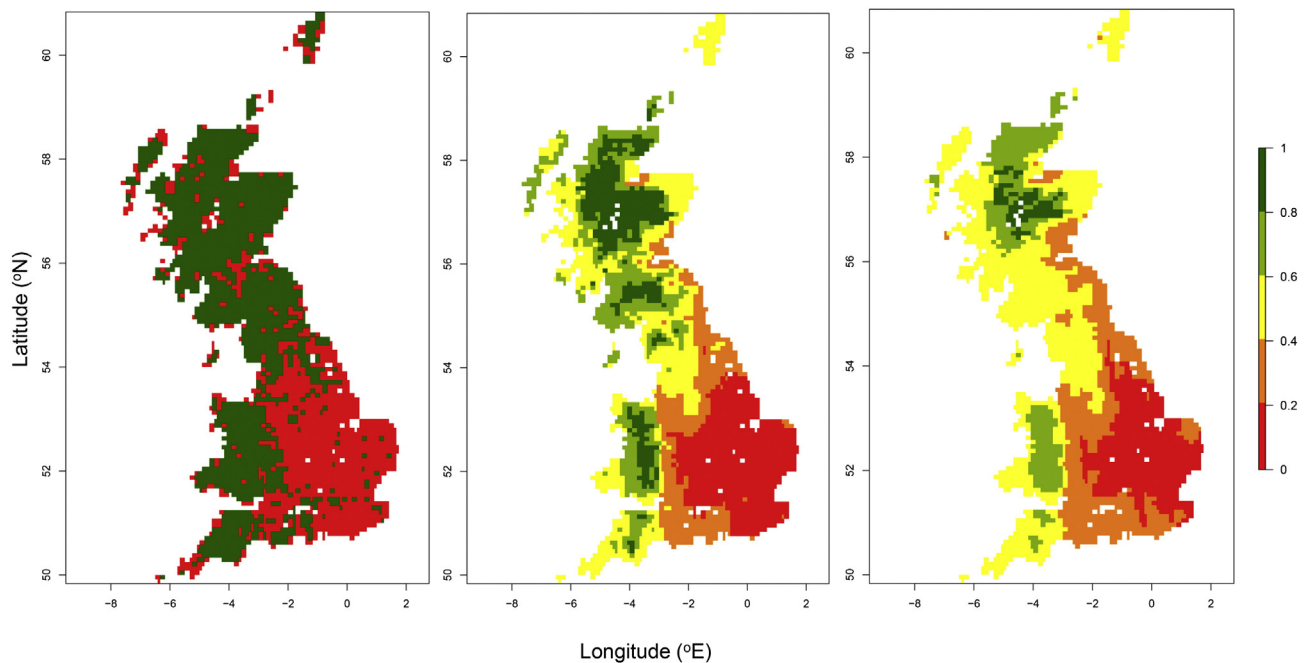
Fig. 1. Current spatial distribution of Atlantic salmon *Salmo salar* in Great Britain (left) and their predicted climate space under BCC-CSM1-1 low emission scenario in 2050 (middle) and high emission in 2070 (right). On the predicted maps, the colour gradient represents the probability (0 to 1) of species presence in the climate change projection according to the legend. (See web version of the article for the full colour version).

13 and 49 km for *E. lucius* (Table 3; Fig. 2). By contrast, if there were no dispersal opportunities from their existing ranges for both species, predictions were for no change to their current distribution (Table 4). For both fishes, annual mean temperature and mean diurnal range of temperature were the most important climatic variables contributing to their predictions, totalling 84.2% for *E. lucius* and 90.2% for *P. fluviatilis*.

The outputs of the ensemble models for the cyprinid fishes revealed varying predictions, with some species predicted to undergo considerable expansions in their climate spaces, including *S. erythrophthalmus* (77 to 177%), *R. rutilus* (44 to 88%) and *A. brama* (80 to 143%) (Table 2; Online Appendices 1,2), with centroid displacements all in a north-westerly direction (*S. erythrophthalmus*: 29 to 115 km; *R. rutilus*: 75 to 121 km; *A. brama*: 54 to 117 km; Table 3; Ruiz-Navarro et al., 2016). Predictions for *C. carpio* were an expanded climate space of between 68 and 136%, with centroid displacement of between 64 and 105 km (Tables 2, 3; Figs. 2, 3). For *S. cephalus*, climate space constriction of between 19 and 82% was predicted (Table 2), with centroid displacement of up to 398 km (Table 3; Fig. 2) (Ruiz-Navarro et al., 2016). For *C. carassius*, *L. leuciscus* and *G. gobio*, predictions varied with the projected climate change scenario, covering both climate space expansion and constriction depending on the climate change scenario (Tables 2, 3; Fig. 2; Online Appendices 1,2). For *C. carassius*, expansions were generally predicted under high emissions and constriction under some low emissions, with the converse for *L. leuciscus* and *G. gobio* (Tables 2, 3; Online Appendices 1,2; Ruiz-Navarro et al., 2016).

These climate niche predictions were also reflected in their dispersal predictions; for species whose climate niches were predicted to expand (Table 3), such as *R. rutilus* and *C. carpio*, there would be no change in their current range if there were no dispersal opportunities available (Table 4). Under full dispersal opportunities, their distributions would increase given their predicted increases in climate niche (Table 4). For species where predictions for their climate niches were decreases, then there was a general predicted decrease in their distribution under no dispersal, but this was lessened under full dispersal (Table 4). For *S. cephalus* and *G. gobio* under no dispersal and high emission scenarios for 2070, some predictions were for extinction from Britain, highlighting the importance of dispersal opportunities for some species to persist (Table 4). Annual mean temperature was the most

important climatic variable in the model predictions of the cyprinid fishes, ranging from 47.9% for *C. carassius* to 71.7% for *L. leuciscus* (Table 5). Its importance for *C. carpio* was also relatively high (70.3%). The combined importance of annual mean temperature and mean diurnal range of temperature ranged between 61.6 and 94.4% across the species (Table 5).

4. Discussion

Building bioclimate models for a range of freshwater fishes in Great Britain under current and future climate scenarios predicted that the climate space of each species would shift, with centroid displacement always in a north-westerly direction. Predictions revealed that even under low emission climate change scenarios and the two dispersal scenarios, alterations in climate space were generally consistent at the family level, with constriction for the freshwater life-stages of native salmonid fishes and a large increase in the climate space of most cyprinid species, including the non-native *C. carpio*, other than under the no dispersal scenario when their distribution would be unchanged. Across all the modelled fishes, annual mean temperature was the most important variable in the ensemble model predictions. There was, however, some inter-family variability across the importance of the climatic variables, with a combination of annual mean precipitation and temperature variables being most important for the two salmonid species. For all other modelled species, temperature variables were most important, with their combined importance to the ensemble models being a minimum of 92%. The limitation of the modelling architecture to the use of only two dispersal scenarios limited the distribution predictions to scenarios of no dispersal and full dispersal. It is highly probable that some dispersal within and between some catchments of species will occur naturally and/or by anthropogenic means (Conti et al., 2015). This is thus a limitation of the method used and so it is recommended that future work incorporates the ability of freshwater fish to disperse in relation to hydrological connectivity and the changes in their environments.

The modelling approach was based on bioclimatic variables, using the assumption that the influence of climate on the biology and ecology of the fishes was the key determinant of their distribution pattern (Woodward and Beerling, 1997; Hampe, 2004). It is important,

Table 3
Location (latitude and longitude, decimal degrees) of the centroids of the original distribution of the model fishes and predicted changes in projected emission scenarios (ES) (km, and bearing in arc degrees considering 0° the north and increasing values in a clockwise direction).

Species	Original		Year	Low ES				High ES			
	Lat	Long		Distance	Lat (t)	Long (t)	Bearing	Distance	Lat (t)	Long (t)	Bearing
(a) BCC-CSM1-1											
S. trutta	54.228347	−2.905277	2050	146	−15.67[b]	15.58[b]	339.2	174	−18.66[b]	16.93[b]	341.0
			2070	136	−14.72[b]	14.33[b]	339.4	225	−23.56[b]	16.80[b]	344.5
S. salar	54.913361	−3.590507	2050	84	−6.76[b]	11.65[b]	334.1	86	−5.34[b]	14.71[b]	325.2
			2070	78	−5.88[b]	11.88[b]	331.9	114	−6.86[b]	11.27[b]	340.8
P. fluviatilis	53.144356	−1.758949	2050	40	−5.35[b]	0.79	355.5	62	−8.02[b]	3.91[b]	345.4
			2070	57	−7.54[b]	1.89	352.3	63	−8.15[b]	3.63[b]	346.7
E. lucius	53.338692	−1.818006	2050	13	−1.64	−0.48	8.8	32	−3.91[b]	1.61	347.8
			2070	33	−4.11[b]	0.09	359.3	33	−4.10[b]	1.36	350.2
C. carassius	52.539497	−1.026232	2050	93	11.21[b]	−5.64[b]	158.2	44	6.08[b]	0.61	184.4
			2070	58	5.67[b]	0.93	186.6	60	8.24[b]	1.07	186.0
S. erythrophthalmus	52.52853	−1.169132	2050	29	−3.46[b]	3.64[b]	323.8	68	−7.31[b]	9.81[b]	317.0
			2070	41	−5.27[b]	4.20[b]	330.9	71	−7.57[b]	10.49[b]	316.1
R. rutilus[c]	52.777101	−1.497009	2050	75	−10.50[a]	5.40[a]	343.8	97	−13.20[a]	8.60[a]	340.1
			2070	89	−12.40[a]	6.10[a]	344.6	101	−13.70[a]	8.60[a]	340.8
S. cephalus[c]	52.510828	−1.262286	2050	178	−16.60[a]	12.00[a]	344.4	361	−37.50[a]	28.40[a]	343.2
			2070	175	−19.07[a]	15.70[a]	340.3	370	−38.50[a]	26.10[a]	343.1
A. brama[c]	52.599898	−1.185012	2050	74	−9.91[a]	6.40[a]	338.4	102	−13.50[a]	10.00[a]	335.9
			2070	89	−12.13[a]	7.50[a]	339.4	112	−14.90[a]	10.80[a]	336.7
L. leuciscus[c]	52.467966	−1.228179	2050	59	−8.20[a]	−2.80[a]	11.7	95	−12.00[a]	0.01	359.9
			2070	76	−11.25[a]	−1.40[a]	4.3	168	−16.90[a]	4.40[a]	352.6
G. gobio[c]	52.534677	−1.286165	2050	135	−17.60[a]	2.70[a]	355.1	245	−21.80[a]	9.80[a]	347.6
			2070	108	−15.40[a]	2.50[a]	354.6	244	−19.80[a]	9.90[a]	347.2
C. carpio	52.552294	−1.286484	2050	64	−8.76[b]	3.72[b]	345.4	101	−13.55[b]	8.40[b]	339.4
			2070	78	−10.71[b]	5.05[b]	343.8	105	−14.05[b]	8.68[b]	339.6
(b) HadGEM2-AO											
S. trutta	54.228347	−2.905277	2050	168	−18.53[b]	16.35[b]	341.0	195	−21.89[b]	17.51[b]	342.3
			2070	130	−13.59[b]	15.90[b]	336.3	243	−26.88[b]	20.67[b]	342.5
S. salar	54.913361	−3.590507	2050	170	−13.29[b]	15.42[b]	340.4	236	−19.18[b]	17.88[b]	342.5
			2070	145	−11.14[b]	15.75[b]	337.2	293	−26.39[b]	22.71[b]	340.4
P. fluviatilis	53.144356	−1.758949	2050	56	−6.74[b]	6.86[b]	330.8	65	−7.86[b]	7.71[b]	332.0
			2070	50	−5.99[b]	6.37[b]	329.4	78	−9.31[b]	8.92[b]	333.1
E. lucius	53.338692	−1.818006	2050	35	−3.41[b]	5.47[b]	319.4	38	−3.93[b]	5.52[b]	323.3
			2070	29	−2.55[b]	5.03[b]	313.0	49	−5.05[b]	7.04[b]	323.9
C. carassius	52.539497	−1.026232	2050	47	5.05[b]	5.89[b]	222.4	50	−4.62[b]	6.83[b]	313.7
			2070	44	4.35[b]	5.84[b]	226.4	112	−11.67[b]	13.15[b]	322.7
S. erythrophthalmus	52.52853	−1.169132	2050	52	−3.00[b]	9.91[b]	292.0	74	−7.93[b]	10.93[b]	316.0
			2070	45	−1.31	8.99[b]	280.7	115	−13.27[b]	14.99[b]	323.0
R. rutilus[c]	52.777101	−1.497009	2050	84	−10.92[b]	10.60[b]	330.5	99	−12.93[b]	11.80[b]	332.4
			2070	77	−9.99[b]	9.93[b]	329.5	121	−15.73[b]	13.86[b]	334.0
S. cephalus[c]	52.510828	−1.262286	2050	265	−32.42[b]	23.85[b]	340.0	342	−38.97[b]	30.54[b]	341.0
			2070	168	−21.14[b]	19.60[b]	332.9	398	−38.30[b]	30.34[b]	341.0
A. brama[c]	52.599898	−1.185012	2050	70	−7.97[b]	11.11[b]	317.6	93	−11.55[b]	12.81[b]	325.2
			2070	54	−5.36[b]	9.87[b]	308.2	117	−14.55[b]	15.14[b]	327.7
L. leuciscus[c]	52.467966	−1.185012	2050	177	−21.92[b]	3.63[b]	354.3	219	−22.13[b]	9.65[b]	347.6
			2070	95	−13.85[b]	2.64[b]	353.0	336	−13.37[b]	4.27[b]	350.2
G. gobio	52.534677	−1.286165	2050	226	−28.69[b]	12.37[b]	345.6	291	−28.82[b]	15.28[b]	345.1
			2070	138	−19.35[b]	9.75[b]	342.1	505	−35.30[b]	28.22[b]	344.4
C. carpio	52.552294	−1.286484	2050	72	−8.79[b]	9.45[b]	325.2	97	−12.45[b]	11.20[b]	330.7
			2070	48	−5.00[b]	8.20[b]	311.1	117	−14.79[b]	13.42[b]	331.1

[a] $p \leq 0.05$.
[b] $p \leq 0.01$.
[c] Ruiz-Navarro et al. (2016).

therefore, to also acknowledge other factors that could also have influenced these distributions. The strength of competitive interactions between species might alter under the new conditions and also potentially lead to novel interactions, thus impacting community structure and thus species' distributions (Van Zuiden et al., 2016). Where species such as C. carpio establish, their ability to increase water turbidity through foraging might adversely impact the persistence of sight feeding piscivores such as E. lucius (Matsuzaki et al., 2007, 2009). Long-term changes in the abiotic and biotic characteristics of British freshwaters include river impoundments, including weir construction impacting migration (especially in the 1900s) (Higgs and Petts, 1988), chronic pollution, impacting nutrient loading and eutrophication (Amisah and Cowx, 2000), and changes in land-use and agricultural practises, altering riparian vegetation (Johnes, 1996; Whitehead et al.,

2002). Whilst all these extant issues can profoundly alter fish communities, their impacts in Britain mainly affect fish abundance, community structure and life history traits (e.g. Beardsley and Britton, 2012), rather than presence/absence. We thus suggest that bio-climate relationships remain an important component in determining freshwater fish distributions in Britain, especially for the species that were modelled.

The assumption that the bioclimate models were suitable for use in the study was supported by their predictions being highly consistent with those from other fish-based climate change studies. These generally provide strong evidence from both freshwater and marine systems that range changes will occur in most fishes due to climate change (Jackson and Mandrak, 2002; Chu et al., 2005; Rahel and Olden, 2008; Jones et al., 2013; Elliott et al., 2015). Whilst the direction and magnitude of range shifts are shaped by the species-specific sensitivity to
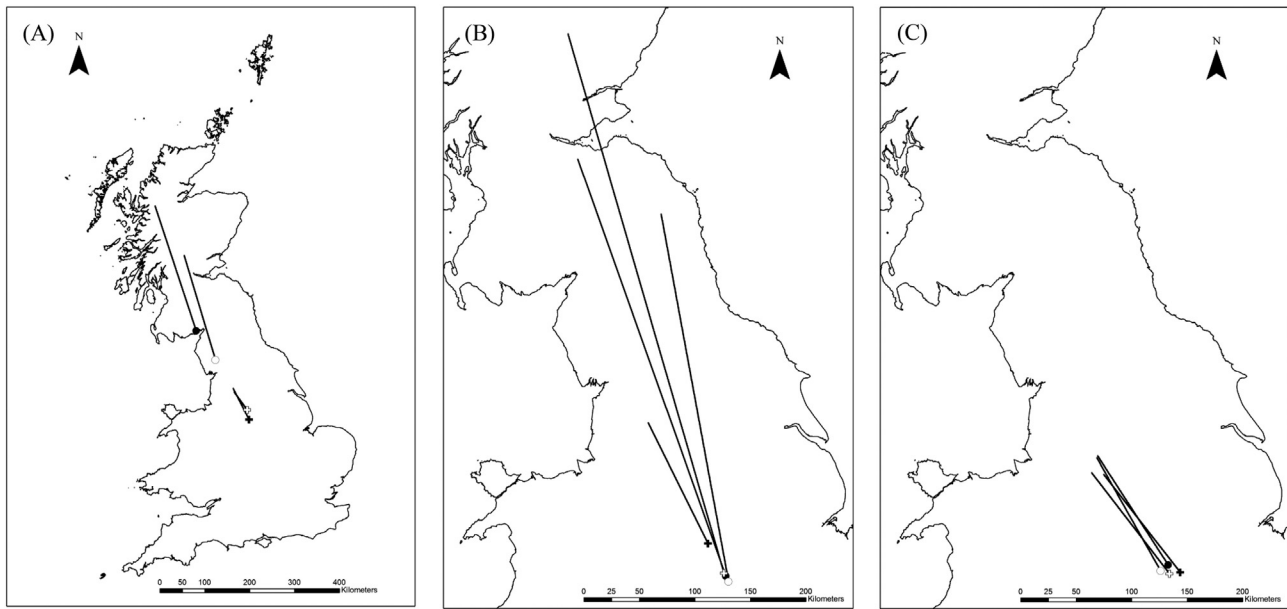
Fig. 2. The extent of centroid displacement, all in a generally north-westerly direction, for (A) *Esox lucius* (clear cross), *Perca fluviatilis* (black cross), *Salmo salar* (filled circle) and *Salmo trutta* (clear circle); (B) *Gobio gobio* (clear cross), *Rutilus rutilus* (black cross), *Squalius cephalus* (filled circle) and *Leuciscus leuciscus* (clear circle); and (C) *Scardinius erythrophthalmus* (clear cross), *Carassius carassius* (black cross), *Abramis brama* (filled circle) and *Cyprinus carpio* (clear circle).

the changes (e.g. their physiological tolerance, resilience and potential to adapt) (Graham and Harrod, 2009; Comte and Grenouillet, 2015), the general pattern over a wide range of terrestrial and aquatic taxa is a pole-ward and altitudinal range shift as species track their thermal niche (e.g. Chen et al., 2011; Melles et al., 2011), including plants (Corlett and Westcott, 2013) and insects (Forister et al., 2010). The drivers of these range changes can be complex, with Conti et al. (2015) suggesting that where species had expanding ranges, this was influenced more by changes in the seasonality of temperatures, whereas where ranges contract, it is due to the interaction of temperature change and alterations in precipitation patterns. Indeed, the importance of annual mean precipitation and temperature variables for the predicted range contractions of the salmonids was consistent with this. For *G. gobio* and *L. leuciscus*, predictions suggested some temperature thresholds might exist, given their predicted expansions of climate space under low emission projections of climate space but constrictions under high emissions.

The predicted constrictions in the climate space of the salmonid species, especially under high emission scenarios, were consistent with them being 'cold-water' fishes with relatively low thermal optima (Rahel and Olden, 2008). Across their global range, there are substantial concerns for the long-term persistence of salmonid fishes in many regions (e.g. Chu et al., 2005; Battin et al., 2007; Ficke et al., 2007; Almodóvar et al., 2012). Nevertheless, in Great Britain, the projected changes in their climate spaces suggest that even in high emission scenarios there are likely to be some rivers at northern latitudes where sustainable populations are able to survive. However, their populations further south are likely to be under considerable threat and where populations could persist, such as in some upland rivers in Southwest England, studies suggest there will be considerable shifts in their biology and ecology due to the combination of increasing temperatures and shifts in precipitation patterns. For example, Jonsson and Jonsson (2009) predicted that for both *S. salar* and *S. trutta*, their traits of age at first maturity, longevity and fecundity would decrease with increasing temperatures. Should changing temperature and rainfall patterns shift the timing of smolt migration to earlier in the year, there could be implications for their marine survival, as smolts in cohorts that emigrate later tend to have increased sea survival rates (Kennedy and Crozier, 2010). Whilst Elliott and Elliott (2010) predicted that *S. trutta*

growth could benefit from small increases in temperature (<2·5 °C), increases of >3 °C could result in negative growth consequences. Jensen et al. (2008) suggested, however, that *S. trutta* populations are likely to have some potential for adapting to changing temperature regimes. In combination, this suggests some persistence in native salmonid populations might be evident in Britain under projected climate changes, but their life histories traits and migration strategies will be altered, and they could potentially have lower sea survival.

The predicted range changes for the cyprinid fishes varied by species, but most had increased climate space, with this space shifting into regions into northern and western Britain where they are not currently present. Only under a scenario of no dispersal did the predicted future distribution of most species match that of their current distribution. These predictions, where mean annual temperature was the most important climatic variable in all cases, were also consistent with other studies and aligned to these fishes often preferring warmer waters to salmonids. For example, they were consistent with those of Graham and Harrod (2009) and Elliott et al. (2015), who both highlighted that species such as *R. rutilus* in Great Britain would be strongly favoured under climate change, with potential for invasions into non-indigenous areas. Of arguably greater concern were, however, the predictions for *C. carpio*, a fish typically considered as preferring water temperatures above 20 °C (Britton et al., 2007). This fish is already recognised as invasive globally (e.g. Koehn, 2004; Zambrano et al., 2006; Britton et al., 2007). Their range in Great Britain is already widespread, being present in the majority of river catchments in England following their high stocking pressure into lake fisheries and their subsequent escape during floods (Britton et al., 2010). This should be a conservation and ecological concern, as under favorable thermal conditions the species is highly invasive (Smith and Walker, 2004; Oyugi et al., 2011), with impacts including substantial declines of submerged vegetation (Williams et al., 2002; Britton et al., 2007) and the resuspension of sediments that increase water turbidity (Lougheed et al., 2004; Matsuzaki et al., 2007, 2009).

In many cases, the projected rapidity of projected change will exceed the ability of species to adapt or disperse to more climatically favorable surroundings. This has resulted in debate over the appropriateness of managed relocations (MR) of species to locations where their future persistence may be more probable (e.g. Lawler and Olden, 2011; Pérez

Table 4

Grade of change (%) in the number of squares occupied by the species for each projected future scenario under full and no dispersal scenarios. Low ES: low emissions scenario; High ES: high emissions scenario. (See Online Appendix 1 for full table including changes in the numbers of occupied squares).

(a) BCC-CSM1-1

Species	Current (Predicted squares)	Prediction year	Full dispersal				No dispersal			
			Low ES (squares)	Change (%)	High ES (squares)	Change (%)	Low ES (squares)	Change (%)	High ES (squares)	Change (%)
S. trutta	2435	2050	1541	−37	1334	−45	1541	−37	1334	−45
		2070	1584	−35	994	−59	1584	−35	994	−59
S. salar	1503	2050	853	−43	616	−59	849	−44	615	−59
		2070	774	−49	420	−72	773	−49	420	−72
P. fluviatilis	1121	2050	1658	48	1824	63	1121	0	1121	0
		2070	1697	51	1818	62	1113	−1	1121	0
E. lucius	1066	2050	1603	50	1746	64	1059	−1	1066	0
		2070	1619	52	1746	64	1048	−2	1066	0
C. carassius	174	2050	330	90	766	340	95	−45	102	−41
		2070	261	50	671	286	91	−48	97	−44
S. erythrophthalmus	547	2050	1294	137	1631	198	547	0	547	0
		2070	1348	146	1689	209	547	0	547	0
R. rutilus	1073	2050	1667	55	1826	70	1073	0	1070	0
		2070	1693	58	1832	71	1072	0	1070	0
S. cephalus	801	2050	452	−44	217	−73	231	−71	1	−100
		2070	627	−22	139	−83	280	−65	0	−100
C. carpio	796	2050	1409	77	1682	111	796	0	793	0
		2070	1492	87	1703	114	796	0	793	0
A. brama	785	2050	1452	85	1670	113	785	0	785	0
		2070	1526	94	1726	120	785	0	785	0
L. leuciscus	894	2050	907	1	771	−14	706	−21	540	−40
		2070	986	10	455	−49	728	−19	276	−69
G. gobio	909	2050	847	−7	406	−55	534	−41	146	−84
		2070	1104	21	314	−65	718	−21	122	−87

(b) HadGEM2-AO

Species	Current (squares)	Prediction year	Full dispersal				No dispersal			
			Low ES (squares)	Change (%)	High ES (squares)	Change (%)	Low ES (squares)	Change (%)	High ES (squares)	Change (%)
S. trutta	2435	2050	1459	−40	1345	−45	1459	−40	1345	−45
		2070	1606	−34	1065	−56	1606	−34	1065	−56
S. salar	1503	2050	707	−53	504	−66	696	−54	496	−67
		2070	818	−46	324	−78	800	−47	259	−83
P. fluviatilis	1121	2050	1982	77	2033	81	1121	0	1121	0
		2070	1943	73	2118	89	1121	0	1121	0
E. lucius	1066	2050	1955	83	1948	83	1063	0	1053	−1
		2070	1882	77	2056	93	1052	−1	1056	−1
C. carassius	174	2050	1034	494	1313	655	110	−37	156	−10
		2070	1013	482	1823	948	107	−39	159	−9
S. erythrophthalmus	547	2050	1607	194	1714	213	547	0	547	0
		2070	1527	179	2032	271	547	0	547	0
R. rutilus	1073	2050	1932	80	2000	86	1073	0	1073	0
		2070	1884	76	2126	98	1073	0	1073	0
S. cephalus	801	2050	637	−20	479	−40	124	−85	21	−97
		2070	764	−5	174	−78	313	−61	0	−100
C. carpio	796	2050	1695	113	1839	131	796	0	796	0
		2070	1573	98	1979	149	796	0	796	0
A. brama	785	2050	1680	114	1811	131	785	0	785	0
		2070	1581	101	1964	150	785	0	785	0
L. leuciscus	894	2050	695	−22	596	−33	359	−60	212	−76
		2070	905	1	99	−89	276	−69	24	−97
G. gobio	909	2050	722	−21	489	−46	246	−73	101	−89
		2070	985	8	76	−92	490	−46	0	−100

et al., 2012; Klenk and Larson, 2013). Olden et al. (2011) argued that due to the constrained existence of freshwater organisms within highly dendritic networks, MR should represent a useful conservation strategy, but with the caveat that the properties of freshwaters also increases the probability of unintended ecological consequences. They concluded that species with a high probability of unintended effects to recipient ecosystems should not be used in MR (Olden et al., 2011). These conclusions have potentially high applicability to the results of the bioclimate models presented here. These suggested that a range of conservation measures is required across the modelled species. These include the prevention of translocation and invasion of C. carpio, R. rutilus and S. erythrophthalmus in northern latitudes, such as via regulatory

measures (Hickley and Chare, 2004; Winfield et al., 2010). They also include conserving climate-vulnerable species, such as S. trutta, and S. salar. Where their local populations become extirpated due to climate change then MR could be considered if efforts are taken to reduce temperature and precipitation impacts, with the latter likely to relate to low flow issues in summer months (Johnson et al., 2009). The MR would then ideally use fish from the same basin to avoid potential genetic issues (Griffiths et al., 2009).

Should MR be argued as an undesirable conservation action for salmonid fishes in Britain, allied to the full dispersal predictions indicating similar decreases in distribution to the no dispersal predictions, then alternative conservation measures would be required. In areas predicted

Table 5
Importance of each climatic variable, expressed as proportion of the total importance (%), in the ensemble model predictions of the shifts in climate space per species, with the overall mean provided per climatic variable. AMT: annual mean temperature; MDRT: mean diurnal range of temperature: IT: isothermality; MTWQ: mean temperature of wettest quarter; MTDQ: mean temperature of driest quarter; and AP: annual precipitation.

Species	Proportion of model prediction explained by climatic variable (%)					
	AMT	MDRT	IT	MTWQ	MTDQ	AP
S. trutta	23.8	8.6	3.2	24.4	6.3	33.7
S. salar	49.9	10.5	2.9	1.6	1.2	34.0
P. fluviatilis	43.5	46.7	1.6	0.5	2.4	5.2
E. lucius	30.7	53.5	3.5	1.7	2.7	8.0
C. carassius	47.9	13.7	2.3	4.1	27.5	4.5
S. erythrophthalmus	65.8	17.9	5.3	1.9	4.5	4.6
R. rutilus	58.3	34.4	1.4	0.2	3.1	2.6
S. cephalus	61.2	33.2	0.7	0.8	2.8	1.3
C. carpio	70.3	20.0	0.6	0.7	6.3	2.1
A. brama	68.2	23.9	0.5	0.8	3.5	3.2
L. leuciscus	71.7	19.6	1.3	1.2	1.5	4.7
G. gobio	70.6	23.7	1.2	0.8	2.0	1.7
Mean (±SE)	55.2 ± 4.7	25.5 ± 4.0	2.0 ± 0.4	3.2 ± 1.9	5.3 ± 2.1	8.8 ± 3.4

to be on the edge or outside of the future climate space of these fishes, such as many areas of central and southern England, the current in situ conservation management ought to shift away from strategies that are often strongly reliant on stocking rivers with juvenile life stages of hatchery reared fish, especially for *S. salar* (Aprahamian et al., 2003, 2004). Instead, they should focus on physical changes that seek to maintain habitat quantity and quality under low flow scenarios and minimise the concomitant warming of water temperatures as air temperatures increase. For example, Broadmeadow et al. (2011) revealed that increasing levels of riparian woodland prevented water temperatures exceeding lethal limits for *S. trutta* in streams of the New Forest, Southern England via shading, with 20 to 40% shading of the channel effective at preventing thermal limits being reached and 80% shading maintaining the thermal optima for *S. trutta* somatic growth (Broadmeadow et al., 2011). Whilst alterations in riparian shading could have substantial consequences for the trophic interactions of the salmonid populations (e.g. Dineen et al., 2007), it nevertheless could provide considerable

'proofing' against warming that would otherwise result in river temperatures exceeding safe thermal limits. This would then also provide considerable conservation benefits for other threatened freshwater species that will be climate-change stressed, such as white-clawed crayfish *Austropotamobius pallipes* (Capinha et al., 2013). Other possibilities could be to attempt to increase food supply and/or reduce predation pressure, both of which have been postulated as promising methods for maintaining the European Golden Plover *Pluvialis apricaria* under moderate climatic change (Pearce-Higgins, 2011).

In conclusion, there were considerable predicted alterations in the climate spaces of the modelled freshwater fishes in Great Britain. Use of two dispersal scenarios (minimum and maximum) indicated the extent of the potential changes in their distributions. Some caution in their interpretation is warranted in relation to the actuality of their distributions shifting in accordance with these, and they overlook other, non-climate related factors (such as other abiotic factors) and interactions that also influence current distributions and future alterations. Nevertheless, the utility of these models for conservation management is in highlighting the species that are at risk of causing invasions in new locations where dispersal opportunities exist, whether these are natural or anthropogenic. For these species, regulatory and remediation actions should minimise this risk. The models also highlighted that for the modelled salmonid fishes, in situ habitat management can be used to minimise the detrimental impacts of climate change on their distributions, given that MR is unlikely to be successful given the predictions of decreases under the full dispersal scenario. Thus, these models should facilitate a range of management and regulatory tools to be either maintained or implemented across Great Britain that increase the probability of salmonid populations persisting in southern and western regions, and avoid invasions of cyprinid species across northern regions.
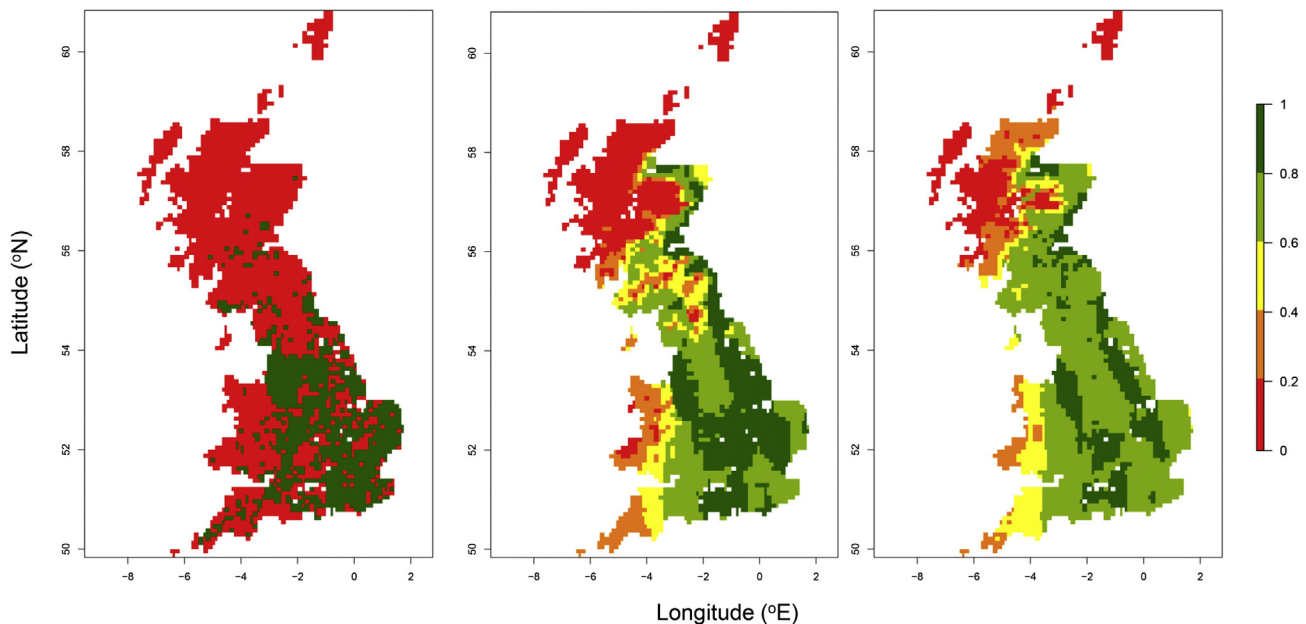
Acknowledgements

Fig. 3. Current spatial distribution of Common carp *Cyprinus carpio* in Great Britain (left) and their predicted climate space under BCC-CSM1-1 low emission scenario in 2050 (middle) and high emission in 2070 (right). On the predicted maps, the colour gradient represents the probability (0 to 1) of species presence in the climate change projection according to the legend. (See web version of the article for the full colour version).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.08.021.

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