Changing UK river temperatures and their impact on fish populations

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INTRODUCTION

River temperature is a key physical parameter of water quality that exerts an influence on almost every aspect of the ecology of lotic systems. In relation to freshwater fishes, a vast literature has accumulated during the last 60 years and more detailing how temperature influences tolerance and mortality; distribution, abundance and diversity; growth, feeding and bioenergetics; reproduction and embryonic development; swimming, movements and migrations; and disease, parasitism and predation. While temperature is far from being the only factor affecting the ecology of freshwater fishes, it is a very significant and complex variable. Complexity arises because the thermal regime of rivers is highly sensitive to a range of natural factors and human impacts, and is therefore subject to change.

Given the sensitivity of thermal regime to environmental changes, there is considerable interest in how river temperature may respond to changing climate associated with global warming in the future, and what the implications may be for freshwater fishes and other groups. Previous research, much of it in North America, has suggested that river temperatures may rise by 1–9°C during the next 50 years due to rising air temperature caused by increasing concentrations of carbon dioxide and other greenhouse gases in the atmosphere (Stefan and Sinokrot, 1993; Webb, 1996; Cushing, 1997). However, uncertainties attend predictions of future river temperatures because the magnitude and pattern of change over large geographical areas, such as the southern United States, may vary significantly depending on the Global Climate Model being used to simulate future air temperatures (Cooter and Cooter, 1990). In addition, climate change may have an indirect, and less readily predictable, effect on future thermal regime through impacts on river flow, groundwater inputs and temperatures, and the nature and extent of riparian vegetation (Cooter & Cooter, 1990; Meisner, 1990; Jager *et al*., 1999).

The most comprehensive investigation of global warming, thermal regime and fish habitat for rivers in the United States has been undertaken by researchers at the St. Anthony Falls Laboratory, University of Minnesota and the U.S. Environmental Protection Agency (Eaton and Scheller, 1996; Mohseni *et al*., 1998; Mohseni *et al*., 1999; Mohseni *et al*., 2003). Initial studies based on predictions for more than 1700 sites, a linear relationship between water and air temperature and an analysis of maximum weekly temperature tolerance of 57 fish species, indicated that the scenario of a doubling in carbon dioxide would lead to decreases in suitable thermal habitat of 47, 50 and 14% for cold, cool and warm water fish guilds, respectively. However, further consideration of the physics of the water/air temperature relationship (Mohseni and Stefan, 1999) showed that the assumption of linearity could not be sustained at air temperatures in excess of *c*. 25°C because of the effects of evaporational cooling. Therefore in more recent studies, an S-shaped function, in which the rise in water temperature at higher air temperatures is limited by an upper bound calculated for each site (Mohseni *et al*., 2002), has been used to predict the impact of global warming on fish habitat. Results of this work suggest that maximum river temperatures associated with a 2 × CO_2 condition are unlikely to exceed the tolerance of warm water fishes, while decreases in the habitat of cold and cool water fish guilds are likely to be less marked than first thought (Mohseni *et al*., 2003). In addition, it was found that accurate information on minimum, as well as maximum, temperature tolerances was vital to successful prediction of future fish habitat, and in the case of warm water fishes with a 2°C lower temperature constraint, global warming is likely to increase habitat in the United States by 31%.

Studies of the impact of global warming on rivers outside of North America and the potential consequences for freshwater fish have been relatively limited, reflecting in part less extensive networks of sites where river temperature is routinely monitored. An investigation of the River Danube at Linz in Austria suggested that temperature would rise by 2030 in response to higher air temperatures and lower flows but there would be seasonal differences with increases being greatest in November and least in May (Webb and Nobilis, 1994). The role of groundwater in potentially moderating the response of river temperatures to global warming was highlighted by a study of two UK rivers which suggested a rise of 2–4°C in monthly mean air temperature would result in a corresponding increase in monthly mean water temperatures of 1.8–3.6°C for a surface-fed, but only 1.1–2.2°C for a spring-fed, system (Mackey and Berrie, 1992). Further information on variation in future river warming across the UK has been provided by a study based on published relationships between mean monthly water and air temperatures for 36 river sites (Webb, 1992). Results suggested that, by 2050, summer and winter mean water temperatures might increase by 0.6–2.2 and 0.4–2.4°C, respectively, depending on geographical location and river type (Webb, 1992).

Despite investigations of potential changes in growth rates of some fish species as a result of future river warming (e.g. Weatherley *et al*., 1991), there has been little published on how fish habitat might be affected in British rivers. The present study examines the impact of possible rises in river temperature during the present century on 12 fish species representative of cold, cool and warm water guilds in UK rivers.

STUDY SITES AND METHODS

The study was based on 27 river temperature monitoring stations (Table 1) operated by various agencies and institutions distributed across the UK. The availability of sufficient detailed data, in the form of hourly observations or daily mean values, from which to construct representative and reliable relationships between water and air temperature, dictated the selection of sites. Information on air temperature was available from meteorological stations (Table 1) located between 1 and 47 km, with an average of 12 km, from the river monitoring

Table 1. Characteristics of the study rivers and associated air temperature monitoring stations.

No.	*Watercourse*	*Site N.G.R.*	*Drainage Area (km^2)*	*Altitude m)*	*Ground -water[1]*	*Riparian Woodland[2]*	*Air Temp. Site N.G.R.*	*Distance[3] (km)*	*Altitude (m)*
1	River Barle	SS927258	128.0	117	0	60	SS874332	9	348
2	Jackmoor Brook	SX902985	9.8	25	1	80	SY001933	11	32
3	Black Ball Stream	SS835305	2.1	287	0	30	SS874332	5	348
4	River Exe	SS935018	601.0	25	0	20	SY001933	11	32
5	River Test	SU352158	1183.0	5	0	15	SU416112	7	3
6	River Calder	SE409258	936.6	15	1	0	SE561372	19	6
7	River Derwent	SK443328	1175.0	30	0	0	SK384401	9	105
8	River Soar	SK593148	347.4	50	1	10	SK530095	8	119
9	River Derwent	SK341525	760.6	70	0	80	SK349629	10	178
10	River Trent	SK224201	3072.0	43	1	10	SK243155	5	85
11	Afron Hafren	SN843877	3.5	364	1	90	SN911870	7	290
12	Afon Hore	SN845872	3.4	350	1	30	SN911870	7	290
13	River Thames	SU779776	5825.1	35	1	10	SU739719	7	66
14	River Thames	SU914788	6910.0	15	0	0	SU846664	14	74
15	River Thames	SU601818	4348.0	45	1	0	SU846664	29	74
16	River Ouse	SE570554	3315.0	5	1	0	SE492613	10	14
17	River Swale	SE225994	514.7	120	1	35	SE305891	13	32
18	River Aire	SE381285	881.2	15	0	0	SE290339	11	64
19	River Trent	SK807612	11259.0	5	0	0	SK988653	19	68
20	River Don	SE668181	1849.0	5	0	0	SE613372	22	6
21	River Ouse	SE574378	3200.0	5	1	0	SE613372	1	6
22	River Hull	TA055419	993.7	5	0	0	TA083301	12	2
23	River Duddon	SD196897	85.7	15	1	40	SD085931	12	8
24	Trout Beck	NY758335	11.5	535	1	0	NY758328	1	556
25	River Medway	TQ748582	1485.6	5	0	0	TQ630127	47	52
26	River Dee	NO061896	289.0	332	1	30	NO061896	9	339
27	River Halladale	NC892556	204.6	35	1	5	NC842653	11	68

[1] 0 = none or low, 1 = high; [2] % of both sides of upstream 5 km reach with trees, [3] distance between water and air temperature sites

sites. Testing in this and other investigations (e.g. Pilgrim *et al.*, 1998) has demonstrated that the strength of water–air temperature relationships is not affected adversely by a relatively large separation of river and climatological stations.

Previous studies in the United States have suggested that weekly average values are the most suitable descriptor of thermal regime when considering the impact of river temperature on fish habitat. Accordingly, data collected for the study sites were used to construct water–air temperature relationships based on weekly average values derived, in turn, from hourly or daily mean data. Following Mohseni *et al.* (1998), non-linear logistic functions of the form:

$$\mathrm{T_w} = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - \mathrm{T_a})}} \tag{1}$$

where:

$\mathrm{T_w}$ = estimated water temperature
$\mathrm{T_a}$ = measured air temperature
m = estimated minimum water temperature
a = estimated maximum stream temperature
b = air temperature at the inflection point of the function
g = measure of the steepest slope of the function

were used to define an S-shaped relationship between water and air temperature, and were fitted using Microsoft Excel Solver, which employs a nonlinear optimisation code.

Present water temperature conditions at the study sites were defined by applying the water–air temperature relationships to a baseline annual cycle of weekly mean air temperature values averaged over at least five years of record. Future thermal regimes for the study rivers were predicted by applying the water–air temperature relationships to the baseline air temperature data at each station incremented by increases in air temperatures projected by UKCIP for 2020, 2050 and 2080 (Hulme and Jenkins, 1998). This exercise took into account differences in air temperature rises for winter, spring, summer and autumn months, and derived rises relevant to each site according to location in relation to the climate forecast squares used by UKCIP (Figure 1). In the case of rivers in south-west and north-east England, rises were interpolated from adjacent forecast squares. Future water temperatures were predicted on the basis of both a low and a high scenario of greenhouse gas emissions.

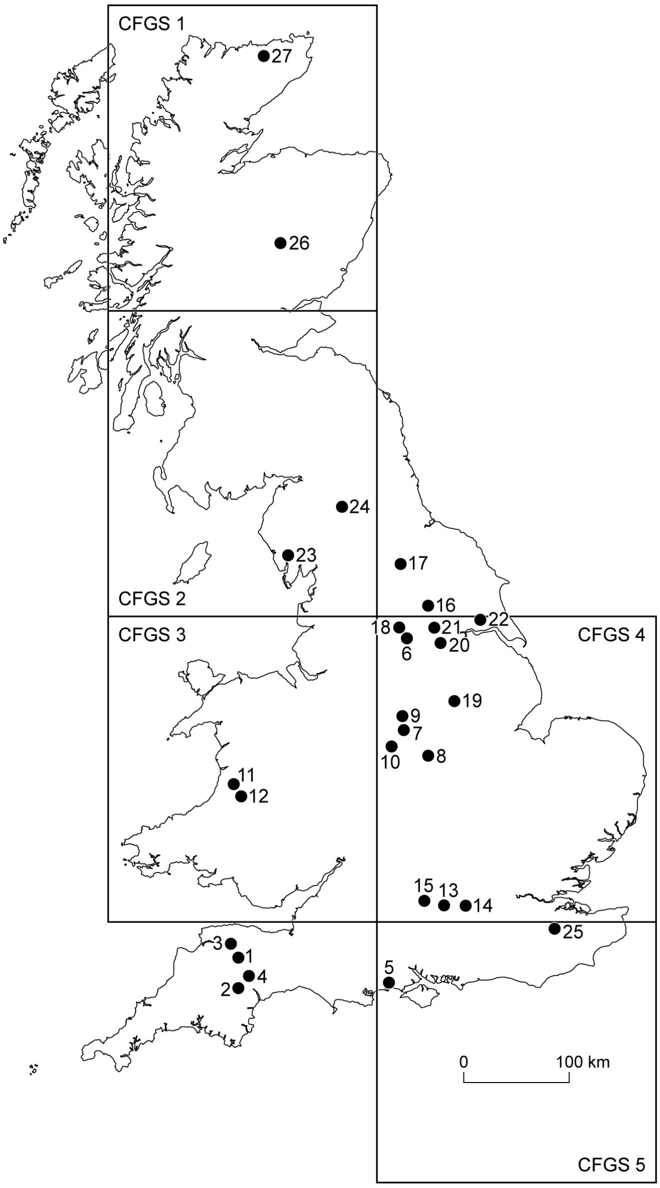

Fig. 1 Location of study sites in relation to UKCIP forecast squares.

Information on the fish species currently present at the study sites was supplied by a range of agencies from the results of electrofishing, netting and angling surveys. Occurrence of fish in the study rivers under future thermal regimes was investigated for 12 species (Table 2). These were chosen because they represented cold, cool and warm water guilds and because sufficient information existed in the literature regarding their thermal limits, from which the potential impact of future changes in river temperatures could be assessed (Table 2). Annual maximum weekly average water temperatures for both present-day and future conditions were compared to the upper physiological and maximum thermal tolerances of different species to identify sites with stressful or inimical temperature conditions. Following, Mohseni and Stefan (2000), rivers experiencing annual minimum weekly average water temperatures below 2°C were considered stressful for warm water species. The extreme values of weekly average water temperatures were also identified for particular periods of the year to identify whether thermal limits for spawning, and in some cases egg incubation, were transgressed for individual species (Table 2). Information on the thermal

Table 2 Criteria used to assess the impact of global warming on the thermal habitat of selected fish species in UK rivers. Sources shown in parentheses.

Species	Physiological thermal tolerance zone (°C)	Maximum thermal tolerance (°C)	Reproductive months investigated (S = spawning, I = egg incubation)	Temperature limits for reproduction (°C)
COLD WATER				
Atlantic salmon (*Salmo salar*)	**7 – 21.9** (Elliott, 1991)	**26** (Elliott, 1991)	ND (S) JF (I)	**0 – 12** (Crisp, 1996)
Brown trout (*Salmo trutta*)	**4 – 19** (Elliott, 1981)	**22.4** (Brungs &Jones, 1977; Cherry *et al*., 1977; Elliott, 1981)	ND (S)	**0 – 11** (Crisp, 1996; Humpesch, 1985; Jungwirth & Winkler, 1984)
Grayling (Mallett *et al*., 1999) (*Thymallus thymallus*)	**4.5 – 21** (Coutant, 1977)	**25**	MJ (I)	**4.1 – 17.5** (Humpesch, 1985)
COOL WATER				
Minnow (*Phoxinus phoxinus*)			MJ (I)	**11 - 22** (Mann, 1996)
Perch (*Perca fluviatilis*)	**28** (Horoszewicz, 1973; Brungs & Jones, 1977)		MA (S)	**6 – 15** (Mann, 1996)
Pike (*Esox lucius*)	**25** (Headrick & Carline, 1993)	**28** (Brungs & Jones, 1977; Eaton & Scheller, 1996)	MA (S)	**4 – 18** (Brungs & Jones, 1977; Hokanson *et al*., 1973)
Roach (*Rutilus rutilus*)	**11.5 – 27** Alabaster& Lloyd, 1982) (Elliott, 1994;		MJ (S)	**7 – 19** (Mann, 1996; Alabaster & Lloyd, 1982)
WARM WATER				
Bleak (*Alburnus alburnus*)	**37.7** (Horoszewicz, 1973)		MJ (S)	**14 – 28** (Alabaster & Lloyd, 1982)
Common Bream (*Abramis brama*)	**28** (Alabaster& Lloyd, 1982)	**30** (Alabaster& Lloyd, 1982)		MJ (S) **12 – 20** (Alabaster & Lloyd, 1982)
Chub (*Leuciscus cephalus*)			MJ (S)	**14 – 22** (Mann, 1996; Alabaster & Lloyd, 1982)
Silver Bream (*Blicca bjoerkna*)			J (S)	**16 -25** (Mann, 1996)
Tench (*Tinca tinca*)	**26** (Coutant, 1977)		JA (S)	**16 -26** (Mann, 1996)

conditions for reproduction is particularly useful in assessing thermal habitat and the viability of fish populations in rivers experiencing future warming.

RESULTS

Future temperatures

Figures 2 and 3 present the predicted increases in annual maximum and minimum weekly average water temperatures for the study sites at three future dates and under both high and low scenarios of global warming. Relatively modest rises in annual maxima are predicted to occur under a scenario of low global warming with an increase of more than 1.5°C forecast for only one site and more than 1°C for only 13 other study rivers by the year 2080. All bar one of the sites are projected to experience increases in annual maxima of less than 1°C by the middle of this century under a scenario of little warming. Significantly greater rises in river temperature are predicted should global warming follow a high scenario. A lowland mainstream site in south-west England (site 4) is forecast to experience a rise in the annual maximum of weekly average values of more than 3.5°C by 2080, and rises in excess of 1.5°C are projected for more than 20 of the study sites (Figure 2). Under the high warming scenario, significant increases in annual maxima are likely to occur earlier in the present century. For example, rises of more than 2°C are predicted by 2050 for 11 sites, and increases of more than 1°C by 2020 for 18 sites. However, predictions suggest that not all rivers in the UK will exhibit significant changes in temperature by the end of the century, even under a high warming scenario. For instance, increases of less than 0.5°C are forecast for the River Derwent (site 9) under both scenarios and at all dates.

The projected increases in annual minimum weekly average water temperature (Figure 3) exhibit differences in extent and in pattern of variation between sites, compared to those for annual maxima. Under a scenario of low warming, rises predicted for 2080 do not exceed 1.5°C and are greater than

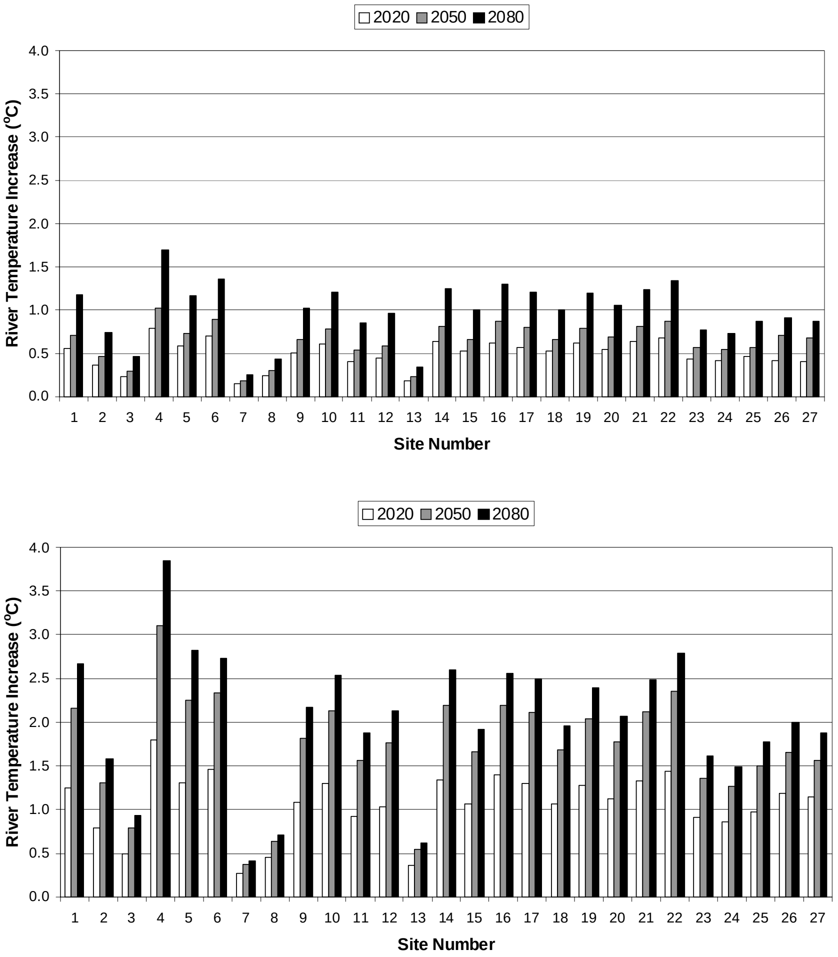

Fig. 2 Predicted increases in annual maximum weekly average temperature at the study sites under scenarios of low (top) and high (bottom) global warming at future dates in the twenty-first century.

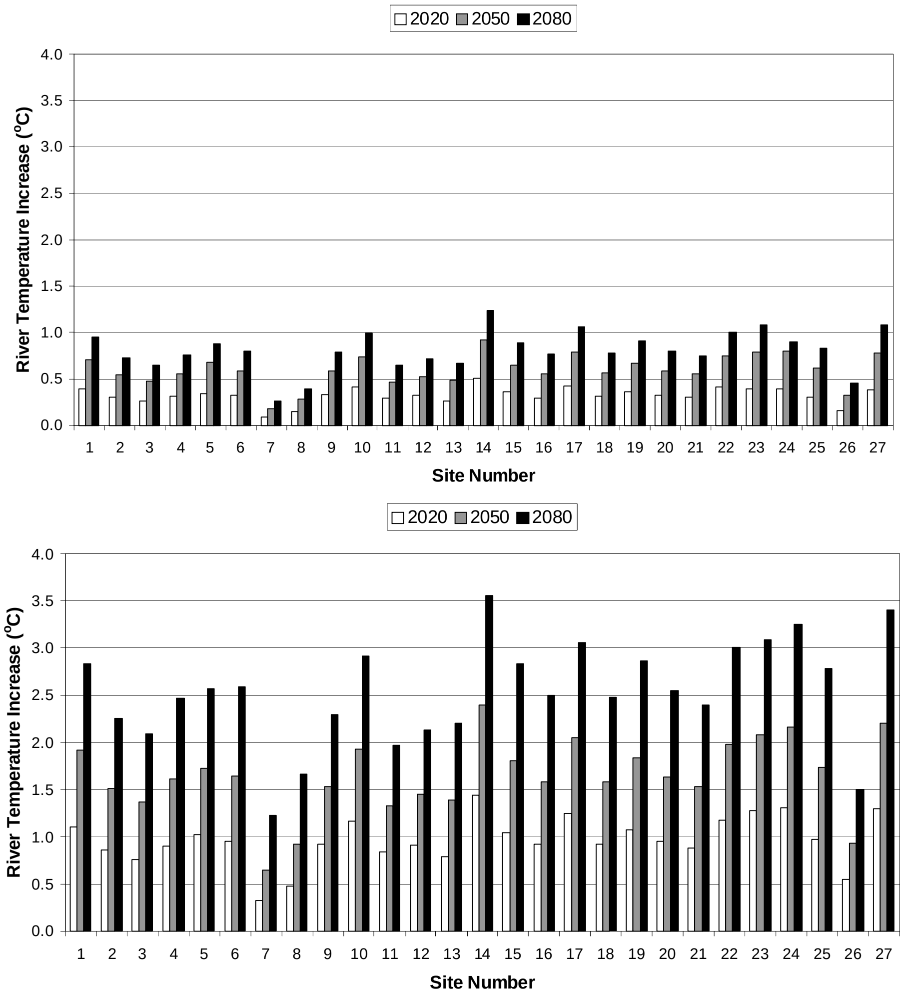

Fig. 3 Predicted increases in annual minimum weekly average temperature at the study sites under scenarios of low (top) and high (bottom) global warming at future dates in the twenty-first century.

1°C at a few sites only; relatively little impact on annual minima is forecast for the first half of the century. Given a scenario of high warming, not only are greater rises in annual minima forecast for UK rivers, but results also indicate an impact which increases markedly over the coming century at all sites (Figure 3). By 2050, a rise of more than 1°C is projected for all bar two rivers, while an increase in excess of 2°C is forecast for 2080 at 23 sites. A rise of more than 3.5°C is predicted for the River Thames (site 14) by 2080 and increases in excess of 3.0°C are projected for 5 other study rivers. Rivers, such as the Derwent (site 7), which exhibit little sensitivity of annual maxima to the effects of global warming, also are associated with relatively low rises in annual minima in the future. However, under a high warming scenario, predictions suggest an increase in annual minimum values at such sites of more than 1°C by the end of the century.

Thermal habitat

Cold water species

Atlantic salmon (*Salmo salar*) is not limited by present temperature conditions at any of the study stations, although this species has been recorded at only nine of the sites (Table 3). Prediction of future conditions suggests that higher river temperatures in winter will be detrimental to spawning and egg incubation, especially under the scenario of high global warming. Results indicate that three of the study rivers currently inhabited by Atlantic salmon will have adverse conditions for spawning and embryo survival in the future: in the case of the River Barle (site 1) and the River Test (site 5) by 2050 but for the River Medway (site 25) by 2020. By 2080, under the scenario of high global warming, 12 of the study rivers are predicted to be uninhabitable, with sites in the south and east of the UK most affected. While the stressful conditions predicted that some reaches in the Trent and the Ouse will also experience summer temperatures that are physiologically damaging to Atlantic salmon. Should a scenario of low global warming apply, habitat for this species will be affected much less seriously. Predictions suggest that conditions would only become detrimental at the station on the River Trent (site 10), which exhibits the highest water temperatures of the study sites under present conditions.

In contrast to Atlantic salmon, the habitat for brown trout (*Salmo trutta*) is limited by present temperature conditions in UK rivers (Table 3). For 7 of the study stations, located in the east of the country, maximum weekly average temperatures exceed those at which brown trout become stressed. With a low scenario of global warming, the number of uninhabitable sites does not change by 2020, but increases to 9 and 12 by 2050 and 2080, respectively. These include the River Test (site 5) and the River Calder (site 6), where this species is currently found. Whereas the detrimental effects of global warming on trout occur under a low scenario through the impact on summer temperatures, predictions indicate that a higher level of warming would also impact adversely on spawning and embryo development of brown trout (Table 3), as well as further exacerbating the problem of physiologically stressful summer temperatures. Under the high scenario, the uninhabitable study sites would rise to 14, 15 and 18, in 2020, 2050 and 2080, respectively, and rivers in south-west England and northern Scotland that currently support brown trout would no longer provide a suitable habitat.

Only three of the stations in the present study have recorded grayling (*Thymallus thymallus*), although the current thermal regime is suitable for this species in all but four of the study rivers (Table 3). In the latter, temperatures are too high during the period of grayling egg incubation between early spring and late summer. Significant change in the thermal habitat for grayling is predicted to occur by 2020, even under a scenario of low global warming, when the number of study sites forecast to become unsuitable is more than double those under present conditions. Under the low scenario, the number of study sites with stressful temperatures for grayling shows a modest increase by 2080, and these rivers remain concentrated in eastern England between the Humber and the Thames. A few sites are predicted to be experiencing physiologically stressful summer temperatures by 2050, as well as thermal conditions inimical to egg incubation. However, the three study rivers where grayling are found presently would still provide a suitable thermal habitat in 2080, if global warming follows the low scenario. Given greater warming, the number of unsuitable habitats rises to 16 by 2080, and from 2050, study rivers along the south coast and in south-west England are predicted to experience conditions stressful to egg incubation. Under the high scenario of global warming, the occurrence of physiologically stressful summer temperatures is predicted to be more common. The River Derwent (site 7) is the only study site, where grayling is recorded currently, which retains a suitable habitat by 2080 under the high warming scenario.

Cool water species

Minnow (*Phoxinus phoxinus*) and pike (*Esox lucius*) were recorded at five and six of the study sites but are not excluded from any of the study rivers by present thermal conditions (Table 4). Furthermore, predictions suggest that rising water temperatures during the next 80 years, even under a scenario of high global warming, will not render the habitat unsuitable for either of these species.

In common with minnow and pike, present temperatures in the study rivers do not limit perch (*Perca fluviatilus*), although this species was recorded only at 14 stations (Table 4) and these were located in southern and eastern England. A scenario of low global warming is predicted to have very little impact on perch, and results suggest that by 2080 only the River Derwent (site 7) will experience spring temperatures that affect the spawning of this species adversely. More significant changes in thermal habitat are forecast to occur under a high scenario of global warming. By 2080, stressful conditions for spawning are predicted for eight of the study rivers, including seven sites where perch are currently recorded.

Roach (*Rutilus rutilus*) also is not limited in any of the study rivers by present thermal regimes, although this species was recorded at only 15 of the stations (Table 4). In common with perch, little impact of rising river temperatures under a scenario of low global warming is apparent. By 2080, only the River Trent (site 10) is predicted to have temperature conditions unfavourable to spawning that takes place during the early summer. The stronger rises in river temperature, that would accompany the scenario of high global warming, are projected to have a more significant effect on roach spawning, especially after 2050. By 2080, unfavourable conditions are predicted for eight sites where roach are found at present (Table 4).

Warm water species

Present thermal conditions are unfavourable to bleak (*Alburnus alburnus*) at 6 of the study sites in the west and north of the country, where temperatures in May and June are too low for spawning (Table 5). In addition, the three northernmost stations experience annual minimum weekly average temperatures that fall below 2^{o}C and are unsuitable for warm water species, including bleak. Although temperatures in the remaining study rivers are favourable, bleak is present at only 6 of the stations. Predictions suggest global warming has the potential to increase the habitat for bleak in UK rivers. Results indicate that under the high warming scenario, only the Afon Hafren (site 11) would remain unfavourable for bleak by 2080, due

Table 3 Thermal habitat for cold water fishes at the study sites under current conditions and under low (L) and high (H) scenarios of global warming at future dates in the twenty-first century.

Site		*Current*	*2020 L*	*2020 H*	*2050 L*	*2050 H*	*2080 L*	*2080 H*
ATLANTIC SALMON								
1	P	F	F	F	F	Sse	F	Sse
2	P	F	F	F	F	F	F	F
3	A	F	F	F	F	F	F	F
4	P	F	F	F	F	F	F	F
5	P	F	F	F	F	Sse	F	Sse
6	A	F	F	F	F	F	F	Sse
7	A	F	F	F	F	Sse	F	Sse
8	A	F	F	F	F	F	F	F
9	A	F	F	F	F	F	F	F
10	A	F	Sse	Sse	Sse	Spse	Sse	Spse
11	A	F	F	F	F	F	F	F
12	A	F	F	F	F	F	F	F
13	A	F	F	F	F	F	F	F
14	A	F	F	F	F	Sse	F	Sse
15	A	F	F	F	F	F	F	Sse
16	A	F	F	F	F	Spse	F	Spse
17	A	F	F	F	F	F	F	F
18	A	F	F	F	F	F	F	Sse
19	A	F	F	F	F	F	F	Sse
20	A	F	F	F	F	F	F	Sse
21	A	F	F	F	F	F	F	F
22	A	F	F	F	F	F	F	F
23	P	F	F	F	F	F	F	F
24	P	F	F	F	F	F	F	F
25	P	F	F	Sse	F	Sse	F	Sse
26	P	F	F	F	F	F	F	F
27	P	F	F	F	F	F	F	F
BROWN TROUT								
1	P	F	F	Sse	F	Sse	F	Spse
2	P	F	F	F	F	F	F	F
3	P	F	F	F	F	F	F	F
4	P	F	F	F	F	Sp	F	Sp
5	P	F	F	Sse	Sse	Sse	Sse	Sse
6	P	F	F	Sp	Sp	Sp	Sp	Spse
7	A	Sp	Sp	Sp	Sp	Spse	Sp	Spse
8	A	F	F	F	F	F	F	Sse
9	P	F	F	F	F	F	F	F
10	A	Spse	Spse	Spse	Spse	Spse	Spse	Spse
11	P	F	F	F	F	F	F	F
12	P	F	F	F	F	F	F	F
13	A	F	F	Sse	F	Sse	F	Sse
14	A	Sp	Sp	Sp	Sp	Spse	Sp	Spse
15	A	F	F	Sp	F	Spse	Sp	Spse
16	A	Sp	Sp	Sp	Sp	Spse	Sp	Spse
17	A	F	F	F	F	F	F	F
18	A	F	F	Sp	F	Spse	Sp	Spse

Table 3 Continued.

Site		Current	2020 L	2020 H	2050 L	2050 H	2080 L	2080 H
19	A	Sp	Sp	Sp	Sp	Spse	Sp	Spse
20	A	Sp	Sp	Sp	Sp	Spse	Sp	Spse
21	A	F	F	Sp	F	Sp	Sp	Spse
22	A	F	F	F	F	F	F	Sse
23	P	F	F	F	F	F	F	F
24	P	F	F	F	F	F	F	F
25	A	Sp	Sp	Spse	Sp	Spse	Sp	Spse
26	P	F	F	F	F	F	F	F
27	P	F	F	F	F	F	F	Sp
Grayling								
1	P	F	F	F	F	Se	F	Se
2	A	F	F	F	F	F	F	F
3	A	F	F	F	F	F	F	F
4	A	F	F	F	F	Se	F	Se
5	P	F	F	F	F	Se	F	Se
6	A	F	Se	Se	Se	Se	Se	Spe
7	A	Se	Se	Se	Se	Se	Se	Se
8	A	F	F	F	F	F	F	Se
9	P	F	F	F	F	F	F	F
10	A	Se	Spe	Spe	Spe	Spe	Spe	Spe
11	A	F	F	F	F	F	F	F
12	A	F	F	F	F	F	F	F
13	A	F	F	F	F	F	F	F
14	A	Se	Se	Se	Se	Spe	Spe	Spe
15	A	F	F	Se	F	Spe	Spe	Spe
16	A	F	Se	Spe	Spe	Spe	Spe	Spe
17	A	F	F	F	F	F	F	F
18	A	F	Se	Se	Se	Se	Se	Se
19	A	Se	Se	Se	Se	Spe	Se	Spe
20	A	F	Se	Se	Se	Spe	Se	Spe
21	A	F	F	F	F	Se	F	Se
22	A	F	F	F	F	Se	F	Spe
23	A	F	F	F	F	F	F	F
24	A	F	F	F	F	F	F	F
25	A	F	Se	Se	Spe	Spe	Spe	Spe
26	A	F	F	F	F	F	F	F
27	A	F	F	F	F	F	F	F

P = currently present, A = currently absent, F = favourable thermal habitat, S = stressful thermal habitat (p = physiologically, s = spawning, e = egg incubation)

Table 4 Thermal habitat for cool water fishes at the study sites under current conditions and under low (L) and high (H) scenarios of global warming at future dates in the twenty-first century.

Site		*Current*	*2020 L*	*2020 H*	*2050 L*	*2050 H*	*2080 L*	*2080 H*
MINNOW/PIKE								
1	P/A	F	F	F	F	F	F	F
2	A/A	F	F	F	F	F	F	F
3	A/A	F	F	F	F	F	F	F
4	P/A	F	F	F	F	F	F	F
5	P/P	F	F	F	F	F	F	F
6	A/A	F	F	F	F	F	F	F
7	A/A	F	F	F	F	F	F	F
8	A/A	F	F	F	F	F	F	F
9	A/P	F	F	F	F	F	F	F
10	A/A	F	F	F	F	F	F	F
11	A/A	F	F	F	F	F	F	F
12	A/A	F	F	F	F	F	F	F
13	A/A	F	F	F	F	F	F	F
14	A/A	F	F	F	F	F	F	F
15	A/A	F	F	F	F	F	F	F
16	P/P	F	F	F	F	F	F	F
17	P/A	F	F	F	F	F	F	F
18	A/A	F	F	F	F	F	F	F
19	A/A	F	F	F	F	F	F	F
20	A/A	F	F	F	F	F	F	F
21	A/P	F	F	F	F	F	F	F
22	A/P	F	F	F	F	F	F	F
23	A/A	F	F	F	F	F	F	F
24	A/A	F	F	F	F	F	F	F
25	A/P	F	F	F	F	F	F	F
26	A/A	F	F	F	F	F	F	F
27	A/A	F	F	F	F	F	F	F
PERCH								
1	A	F	F	F	F	F	F	F
2	A	F	F	F	F	F	F	F
3	A	F	F	F	F	F	F	F
4	A	F	F	F	F	F	F	F
5	A	F	F	F	F	F	F	F
6	P	F	F	F	F	F	F	F
7	P	F	F	Ss	F	Ss	Ss	Ss
8	P	F	F	F	F	F	F	F
9	A	F	F	F	F	F	F	F
10	P	F	F	Ss	F	Ss	F	Ss
11	A	F	F	F	F	F	F	F
12	A	F	F	F	F	F	F	F
13	P	F	F	F	F	F	F	F
14	P	F	F	F	F	F	F	Ss

Table 4 Continued.

Site		*Current*	*2020 L*	*2020 H*	*2050 L*	*2050 H*	*2080 L*	*2080 H*
15	P	F	F	F	F	F	F	F
16	P	F	F	F	F	F	F	Ss
17	P	F	F	F	F	F	F	F
18	A	F	F	F	F	F	F	Ss
19	P	F	F	F	F	F	F	Ss
20	P	F	F	F	F	F	F	Ss
21	P	F	F	F	F	F	F	F
22	P	F	F	F	F	F	F	F
23	A	F	F	F	F	F	F	F
24	A	F	F	F	F	F	F	F
25	P	F	F	F	F	F	F	Ss
26	A	F	F	F	F	F	F	F
27	A	F	F	F	F	F	F	F
Roach								
1	A	F	F	F	F	F	F	F
2	A	F	F	F	F	F	F	F
3	A	F	F	F	F	F	F	F
4	A	F	F	F	F	F	F	F
5	P	F	F	F	F	F	F	F
6	P	F	F	F	F	Ss	F	Ss
7	P	F	F	F	F	F	F	Ss
8	P	F	F	F	F	F	F	F
9	A	F	F	F	F	F	F	F
10	P	F	F	Ss	F	Ss	Ss	Ss
11	A	F	F	F	F	F	F	F
12	A	F	F	F	F	F	F	F
13	A	F	F	F	F	F	F	F
14	P	F	F	F	F	Ss	F	Ss
15	P	F	F	F	F	F	F	F
16	P	F	F	F	F	Ss	F	Ss
17	P	F	F	F	F	F	F	F
18	P	F	F	F	F	F	F	F
19	P	F	F	F	F	Ss	F	Ss
20	P	F	F	F	F	F	F	Ss
21	P	F	F	F	F	F	F	F
22	P	F	F	F	F	F	F	F
23	A	F	F	F	F	F	F	F
24	A	F	F	F	F	F	F	F
25	P	F	F	F	F	F	F	Ss
26	A	F	F	F	F	F	F	F
27	A	F	F	F	F	F	F	F

P = currently present, A = currently absent, F = favourable thermal habitat, S = stressful thermal habitat (p = physiologically, s = spawning, e = egg incubation)

Table 5 Thermal habitat for warm water fishes at the study sites under current conditions and under low (L) and high (H) scenarios of global warming at future dates in the twenty-first century.

Site		*Current*	*2020 L*	*2020 H*	*2050 L*	*2050 H*	*2080 L*	*2080 H*
Bleak/Chub								
1	A/A	F	F	F	F	F	F	F
2	A/A	Ss	Ss	Ss	Ss	F	Ss	F
3	A/A	Ss	Ss	Ss	Ss	F	Ss	F
4	A/A	F	F	F	F	F	F	F
5	A/P	F	F	F	F	F	F	F
6	A/A	F	F	F	F	F	F	F
7	A/P	F	F	F	F	F	F	F
8	A/P	F	F	F	F	F	F	F
9	A/A	F	F	F	F	F	F	F
10	P/P	F	F	F	F	F	F	F
11	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
12	A/A	Ss	Ss	Ss	Ss	F	Ss	F
13	A/A	F	F	F	F	F	F	F
14	P/P	F	F	F	F	F	F	F
15	P/P	F	F	F	F	F	F	F
16	P/P	F	F	F	F	F	F	F
17	A/A	F	F	F	F	F	F	F
18	A/P	F	F	F	F	F	F	F
19	A/P	F	F	F	F	F	F	F
20	A/A	F	F	F	F	F	F	F
21	P/P	F	F	F	F	F	F	F
22	P/A	F	F	F	F	F	F	F
23	A/A	Ss	F	F	F	F	F	F
24	A/A	Sp	F	F	F	F	F	F
25	P/P	F	F	F	F	F	F	F
26	A/A	Sps	Sps	Sps	Sps	Sps	Sps	F
27	A/A	Sp	Sp	F	F	F	F	F
Bream								
1	A	F	F	F	F	F	F	F
2	A	Ss	F	F	F	F	F	F
3	A	F	F	F	F	F	F	F
4	A	F	F	F	F	F	F	F
5	A	F	F	F	F	F	F	F
6	P	F	F	F	F	F	F	F
7	P	F	F	F	F	F	F	F
8	P	F	F	F	F	F	F	F
9	A	F	F	F	F	F	F	F
10	P	F	F	F	F	Ss	F	Ss
11	A	Ss	Ss	F	F	F	F	F
12	A	F	F	F	F	F	F	F
13	P	F	F	F	F	F	F	F
14	P	F	F	F	F	F	F	Ss
15	P	F	F	F	F	F	F	F
16	P	F	F	F	F	F	F	Ss
17	A	F	F	F	F	F	F	F
18	A	F	F	F	F	F	F	F
19	P	F	F	F	F	Ss	F	Ss

Table 5 Continued.

Site		*Current*	*2020 L*	*2020 H*	*2050 L*	*2050 H*	*2080 L*	*2080 H*
20	A	F	F	F	F	F	F	F
21	P	F	F	F	F	F	F	F
22	A	F	F	F	F	F	F	F
23	A	F	F	F	F	F	F	F
24	A	Sp	F	F	F	F	F	F
25	A	F	F	F	F	F	F	F
26	A	Sp	Sp	Sp	Sp	Sp	Sp	F
27	A	Sp	Sp	F	F	F	F	F
SILVER BREAM/ TENCH								
1	A/A	Ss	F	F	F	F	F	F
2	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
3	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
4	A/A	Ss	F	F	F	F	F	F
5	A/A	Ss	F	F	F	F	F	F
6	A/A	F	F	F	F	F	F	F
7	A/P	F	F	F	F	F	F	F
8	A/P	F	F	F	F	F	F	F
9	A/A	Ss	Ss	Ss	Ss	F	Ss	F
10	A/A	F	F	F	F	F	F	F
11	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
12	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
13	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
14	A/A	F	F	F	F	F	F	F
15	A/A	F	F	F	F	F	F	F
16	A/P	F	F	F	F	F	F	F
17	A/A	Ss	Ss	F	F	F	F	F
18	A/A	F	F	F	F	F	F	F
19	A/A	F	F	F	F	F	F	F
20	A/A	F	F	F	F	F	F	F
21	P/A	F	F	F	F	F	F	F
22	A/A	F	F	F	F	F	F	F
23	A/A	Ss	Ss	Ss	Ss	Ss	Ss	Ss
24	A/A	Sps	Ss	Ss	Ss	Ss	Ss	Ss
25	P/A	F	F	F	F	F	F	F
26	A/A	Sps	Sps	Sps	Sps	Sps	Sps	Sps
27	A/A	Sp	Sp	F	F	F	F	F

P = currently present, A = currently absent, F = favourable thermal habitat, S = stressful thermal habitat (p = physiologically, s = spawning, e = egg incubation)

to unsuitable spawning temperatures. The effects of high warming are forecast to be felt as early as 2020 for study rivers in northern England and Scotland where only the River Dee is projected to be unfavourable for bleak because of physiologically stressful winter temperatures and unsuitable thermal conditions for spawning. However, the latter limitation is predicted to remain by 2020 at several study sites in Wales and south-west England (Table 5). Should global warming follow the low scenario, stressful spawning conditions for bleak in these areas will persist till 2080. However, even given the scenario of low warming, study sites in northern England and Scotland would become favourable for this species by 2050, with the exception of the River Dee (site 26). The lower thermal limit for spawning is the same for chub (*Leuciscus cephalus*) and for bleak, so that predictions of habitat suitability under future temperature conditions are identical for these species. However, chub was more commonly recorded under present conditions at the study sites and was found at 11 of the stations (Table 5).

Bream (*Abramis brama*) was present in 10 of the study rivers, but thermal conditions were unfavourable due to low winter temperatures at three northernmost stations and because of temperatures too low for spawning at two sites in Wales and south-west England. Warming under both low and high scenarios is predicted largely to remove the physiologically stress and detrimental conditions for spawning associated with low temperatures, although winter temperatures would not become suitable for bream in the River Dee (site 26) until 2080 and then only if the scenario of high global warming applies. However, as warming affects rivers, especially in eastern England, temperatures may become too high for successful spawning, particularly under the high scenario. In this case, four of the sites where bream are currently present, would have an unfavourable habitat by 2080. The overall effect of high warming on bream would be to transfer unsuitable habitat from the north and west of the country to the south and east.

Silver bream (*Blicca bjoerknal*) was only found at two of the study sites (Table 5) although temperature conditions at present would not be unfavourable for 11 of the study rivers that are located in the east and south of the country. However, the thermal regime of more than half the study rivers is unsuitable currently for this species, largely through temperatures that are too low for successful spawning in the west of the UK and at some sites in the south but also because of the occurrence of physiologically stressful winter temperatures in northern England and Scotland. Higher river temperatures with global warming are predicted to increase habitat for silver bream but many rivers in the west and north of the country will retain a thermal habitat unfavourable to this species. Results show that, even by 2080 under the high scenario, eight of the study stations will have temperatures below the limit for successful spawning. Examining forecasts also suggests that temperature rises occurring between the middle and the end of the present century will have little impact on the availability of habitat for silver bream. Predictions of habitat suitability for tench (*Tinca tinca*) in the study rivers are the same as those for silver bream because these species have the same lower thermal limit for successful spawning. Like silver bream, tench was found under present conditions at a few of the study sites (Table 5).

DISCUSSION

The present study indicates that global warming will cause UK river temperatures to increase during the present century, but the magnitude of the rise and its potential impact on the habitat of freshwater fish will vary from being modest to being very significant depending on which scenario of greenhouse gas emissions, and therefore of global warming, comes to pass. Forecasts of river temperature rises indicate a significant local variability between sites that suggests the impact of climate change and rising air temperature on river thermal regime is mediated by site and catchment characteristics, such as shading from riparian vegetation and the occurrence of groundwater inflows (Erickson and Stefan, 2000). Therefore, while future climate change may show clear regional patterns of variation across the UK, such regularity is not to be expected in river temperature responses.

Perhaps not surprisingly, the results of the present study suggest that future global warming is likely to be detrimental to the habitat of cold water species but generally beneficial to that of warm water guilds. Predictions indicate that higher winter temperatures and adverse effects on spawning are as significant as higher summer temperatures and physiological stresses for winter-spawning species, such as salmon and trout. The effects of higher temperatures on egg incubation, alevin and fry size, and over-winter mortality may also be negative, and warmer waters may additionally have adverse effects on cold water species by inhibiting growth and affecting the intake and resistance to toxins. In contrast, information available on thermal tolerances suggests warm water species such as bleak, tench, bream and chub are prevented from spawning at many of the study sites in western Britain by low temperatures, and it is also likely that summer temperatures are not high enough in these rivers to promote substantial growth of young of the year fish. Rising river temperatures in future will help to ameliorate these adverse conditions and also eventually eradicate the occurrence of minimum temperatures that are lethal to warm water fish from throughout the UK. However, rising water temperatures may adversely affect spawning of some warm water species in parts of the UK.

It should be noted that the present study provides an estimate of only the potential impact of future river temperatures on fish habitat in UK rivers. Many other ecological factors affect the survival of fish and it is difficult to predict how a species may respond to unfavourable thermal regimes. Spring and early summer spawners, such as perch and roach, may be able to shift their spawning seasons to earlier in the year to ameliorate rising temperatures, while some species may be capable of genetic adjustment to increase tolerance to temperatures outside of their usual thermal ranges. Furthermore, changes in thermal regime favouring warmer guilds does not necessarily mean these species will become established, because factors such as presence of migration corridors, availability of appropriate food resources, and the effects of competition and predation will influence the potential for changes in fish distributions. Lastly, there is further scope for refining information on future changes in UK river temperatures by increasing the number of sites investigated, by considering more detailed inter-regional information on climate change, and by developing more sophisticated ways of predicting the river temperature response.

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