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APPLIED ISSUES

Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region

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SUMMARY

1. Temperate regions with fish communities dominated by cold-water species (physiological optima <20 °C) are vulnerable to the effects of warming temperatures caused by climate change, including displacement by non-native cool-water (physiological optima 20–28 °C) and warm-water fishes (physiological optima >28 °C) that are able to establish and invade as the thermal constraints on the expression of their life history traits diminish.
2. England and Wales is a temperate region into which at least 38 freshwater fishes have been introduced, although 14 of these are no longer present. Of the remaining 24 species, some have persisted but failed to establish, some have established populations without becoming invasive and some have become invasive. The aim of the study was to predict the responses of these 24 non-native fishes to the warming temperatures of England and Wales predicted under climate change in 2050.
3. The predictive use of climate-matching models and an air and water temperature regression model suggested that there are six non-native fishes currently persistent but not established in England and Wales whose establishment and subsequent invasion would benefit substantially from the predicted warming temperatures. These included the common carp *Cyprinus carpio* and European catfish *Silurus glanis*, fishes that also exert a relatively high propagule pressure through stocking to support angling and whose spatial distribution is currently increasing significantly, including in open systems.
4. The potential ecological impacts of the combined effects of warming temperatures, current spatial distribution and propagule pressure on the establishment and invasion of *C. carpio* and *S. glanis* were assessed. The ecological consequences of *C. carpio* invasion were assessed as potentially severe in England and Wales, with impacts likely to relate to habitat destruction, macrophyte loss and increased water turbidity. However, evidence of ecological impacts of *S. glanis* elsewhere in their introduced range was less clear and so their potential impacts in England and Wales remain uncertain.

Keywords: *Cyprinus carpio*, global warming, invasion pathway, propagule pressure, *Silurus glanis*.

Introduction

The effects of climate change on biological and ecological processes are likely to interact with other environmental stressors to affect the distribution, abundance and impact of non-native aquatic species

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(Gritti, Smith & Sykes, 2006; Hellmann *et al.*, 2008; Rahel & Olden, 2008). Climate change is likely to facilitate some non-native and non-invasive species to develop invasive populations (Dukes & Mooney, 1999; Hellmann *et al.*, 2008). As climate-change models generally agree of an increasing trend in air temperatures (Johnson *et al.*, 2009), there will be consequent increases in water temperatures and potentially increased hydrological variability. For some fishes, these conditions may favour their reproduction and increase recruitment as thermal constraints on their life history traits diminish (Hellmann *et al.*, 2008). For example, in temperate regions where fish communities are dominated by cold-water species (physiological optima <20 °C), the current temperatures provide an effective filter to the establishment of introduced cool-water (physiological optima 20–28 °C) and warm-water (physiological optima >28 °C) (Magnuson *et al.*, 1997; Rahel & Olden, 2008) fishes. As this filter diminishes with warming temperatures, the opportunity for these introduced fishes to establish is enhanced through their increasing competitive ability and reproductive potential (Graham & Harrod, 2009; Wilson, Nibbelink & Peterson, 2009). Their establishment may also be enhanced by the cold-water species being displaced from their previously suitable, cold habitats because of the warming conditions (Buisson *et al.*, 2008).

Biologists have attempted to predict the range expansions of some aquatic species by projecting current species temperature limits onto maps of future temperature conditions, for example demonstrating that some species may have to move northwards to remain in conditions of their thermal optima (e.g. Lehtonen, 1996; Mohseni, Stefan & Eaton, 2003). However, this generally assumes that species are able to move across physical barriers, an action generally requiring human intervention (Gozlan *et al.*, in press). Thus, it is arguably more important to identify the effect of warming temperatures on non-native species that have already been introduced and then survived in waterbodies in a region, but whose establishment and invasion is currently thermally constrained. This is especially the case where current legislation and environmental policies are effective at preventing further introductions of non-native species into a region. An example is England and Wales, where current legislation and policies are sufficiently strict to minimise the opportunity for new introductions of non-native fishes (Hickley & Chare, 2004). The climate of England and Wales is temperate; temperatures vary with season and latitude, with the mean maximum temperature at the most southerly latitudes (50°N) peaking in August at approximately 21 °C, with the mean minimum temperatures being generally recorded in January and February at approximately 1 to 2 °C (Meteorological Office, 2009a). The warming effects of climate change have also been predicted, with a minimum air temperature increase of 2 °C predicted by 2050 (Meteorological Office, 2009b).

To predict the responses of non-native fishes to warming temperatures in a temperate region, the receiving environment used was England and Wales, and the non-native fishes were those that have already been introduced into these countries. The objectives of the study were to (i) identify the current status of fishes already introduced into England and Wales (according to their distribution, dispersal and establishment of self-sustaining populations); (ii) identify the role of temperature in determining their status in 2009; (iii) predict for which of those introduced, non-established fishes warming temperatures would most enhance their ability to establish and become invasive and (iv) assess the potential severity of the ecological impact of establishment.

Methods

Throughout the article, the following definitions (adapted from Copp *et al.*, 2005a) are used: (i) non-native fish refers to a species, subspecies, race or variety that does not occur naturally in England and Wales but is present in the wild following introduction (i.e. not including closed research facilities and aquaculture sites, Hill *et al.*, 2005), and (ii) invasive species refer to non-native species that reproduce and disperse with or without the aid of humans, in natural or semi-natural habitats, producing a significant change in composition, structure or ecosystem processes, or cause severe economic losses to human activities. The predictions of air temperature increase that were used were a minimum air temperature increase of 2 °C occurring by 2050 (a likely minimum increase that will occur irrespective of emission decreases), with additional scenarios of mean air temperature increases of 3 and 5 °C also used (Meteorological Office, 2009b).

The fish species used for the predictions were selected on the basis of their introduction into England and Wales. These records were collated from a combination of literature sources (cited later) and on data held by the Environment Agency on consented fish stockings into inland waters (excluding aquaculture and research sites) between 1998 and 2008 (Hickley & Chare, 2004). These data provided information on the introductions, current distribution and status (according to their distribution, dispersal and establishment of self-sustaining populations) of these fishes, and for those used to enhance recreational angling, their propagule pressure (the annual number of consented stocking events and total number of individual fish consented for stocking per year). Information on actual recordings of non-native fish in the wild were obtained from data collected during the Environment Agency fisheries monitoring programme conducted between 1980 and 2008 and were expressed as follows: (i) the cumulative annual number of riverine sites where the species was recorded, (ii) the annual number of riverine sites per year where the species was recorded and (iii) the temporal relationship of the annual number of sites where the species was recorded (linear regression). Complementary data sources, including reports from the angling and popular media where appropriate, were used to ensure that all past introductions were assessed (Wheeler & Maitland, 1973; Lever, 1977, 1996; Davies *et al.*, 2004; Hickley & Chare, 2004; Maitland, 2004; Wheeler, Merrett & Quigley, 2004; Hill *et al.*, 2005; Pinder, Gozlan & Britton, 2005; Britton & Davies, 2006, 2007; Copp *et al.*, 2006b; Copp *et al.*, 2006a; Copp, Templeton & Gozlan, 2007). Not considered here are species that have been mentioned in one or more literature sources, but scrutiny of the evidence has either refuted, or raised sufficient doubt, that they were ever introduced (i.e. brown bullhead *Ameiurus nebulosus* (Le Sueur), gibel carp *Carassius gibelio* (Bloch), riffle minnow *Leuciscus souffia* (Risso), smallmouth bass *Micropterus dolomieui* Lacépède). Also ignored are the salmonid species Danube salmon *Hucho hucho* (L.), Dolly Varden charr *Salvelinus malma* (Walbaum) and Lahontan cutthroat trout *Oncorhynchus clarki* (*henshawi*) that have been reported introduced to the British Isles at some time in the past (Maitland, 2004), but details are too scanty to permit further consideration. Species that were identified as having been introduced in past but data suggests they are no longer present were precluded from subsequent predictions.

The introduction and status data were complemented by invasiveness scores from 'FISK' (Fish Invasiveness Scoring Kit; Copp, Garthwaite & Gozlan, 2005b; Copp *et al.*, 2009a). This pre-screening tool for introductions of freshwater fishes assesses the likelihood of species establishment, persistence and the severity of potential environmental impact (Copp *et al.*, 2009a). Species with scores in the 'high risk' category (≥19) were identified as those most likely to incur a substantial ecological impact should they be predicted to subsequently develop invasive populations under warming conditions (Parrott *et al.*, 2009).

To predict the response of the introduced fish to warming temperatures, a two-step approach was followed. The first step was to identify their current thermal compatibility in England and Wales. This was completed using the climate-matching software 'Climatch' (Bomford *et al.*, 2009). This identifies the climate match on a 0 (low match) to 10 (high match) scoring scale of the native range of the non-native fish (user-defined, *Source* region) with that of the receiving environment (user-defined, *Target* region) using a range of user-selected climatic variables from the weather recording stations in the respective regions (Crombie *et al.*, 2008). The climatic variables selected for the models were annual mean temperature, annual temperature range and the temperatures of the warmest month and warmest quarter, and the Euclidean algorithm was used for the calculation (Crombie *et al.*, 2008). The Source regions of the non-native fishes were identified using data sources including Nelson (2006), Fishbase (2009) and Lever (1977, 1996). Where the model predicted a relatively close climate match between the Source and Target regions according to the temperature variables (mean score >7.0), this was interpreted as temperature not being a constraint on the establishment of the species in the Target region. Because of the general relationship of decreasing temperature with increasing latitude (Graham & Harrod, 2009), the presence of differences in air temperature with latitude was initially tested for England and Wales. Daily air temperature data were obtained for 45 weather stations along a latitudinal gradient (50–55°N) from 1990 until 1999, with supplementary data provided on the altitude, longitude and precipitation of each station (National Climatic Data Center, 2009). These data were then grouped by latitude in increments of 2°N (i.e. Group 1: 50–51, Group 2: 52–53 and Group 3: 54–55°N), and a general linear model (GLM) was used to identify significant temperature differences between these groups. The temperature data used were from April until September to represent the period of the fish growth season in England and Wales (Britton, 2007). Altitude, longitude and precipitation were controlled in the model, and pairwise comparisons with Bonferroni adjustments for multiple comparisons used for determining the mean temperature differences and their significance between each group. If tests revealed significant differences in the groups according to latitude, then the groups were used separately in Climatch.

The second step in predicting the response of the introduced fish to warming temperature was to use Climatch predicatively. This could not be performed directly, because Climatch cannot be used to predict the effects of scenarios of warming temperatures in this manner. Thus, the Target region(s) for 2050 were regions identified by their current temperature characteristics being representative of England and Wales in 2050, i.e. with a temperature increase of at least 2 °C. These regions were identified by collating daily air temperature data for 70 weather stations between 1990 and 1999 located on a latitudinal gradient between 40 and 49°N through France and Spain (National Climatic Data Center, 2009). These locations were used so as to minimise any effects of longitude on temperature. For each weather station, supplementary data were provided on its altitude, longitude and precipitation. These data were grouped by latitude in increments of 2°N (Group 4: 40–41, Group 5: 42–43, Group 6: 44–45; Group 7: 46–47; Group 8: 48–49°N) and used in a GLM to compare the temperature profiles of each group with the latitude groups in England and Wales, where altitude, longitude and precipitation were controlled in the model, and pairwise comparisons with Bonferroni adjustments for multiple comparisons used for determining the mean temperature differences and their significance between each group. To provide a range of comparisons between these grouped data, three GLMs were constructed: for daily temperatures in April (current start of fish growth season), July (mid-summer) and September (current end of fish growth season). Where the difference between a group in England and Wales was significantly different by approximately 2 °C in each GLM with a group along the latitudinal gradient, then this was the group used as the Target region in Climatch to represent conditions in 2050. On completion of this for each species, the mean Climatch score in 2009 was plotted against its predicted score in 2050, with the species interpreted as benefitting most from the warming temperatures being those whose mean score was <7.0 in 2009 (relatively poor match) and >7.0 in 2050 (relatively strong match). For these species, data on their current distribution and propagule pressure were then used to rank those species that would most likely develop sustainable populations capable of spreading rapidly.

Given that these predictions were based on air temperature, then the species predicted as most likely to benefit from warming air temperatures were validated by water temperature predictions. Daily water temperature data (nearest 0.1 °C) were collated between 1990 and 1999 for the River Trent, Nottingham and used to predict their level in the 2050s. This was performed using the regression relationship between the daily mean river water temperature (R_T) (dependent variable) and daily mean air temperatures (CET: Central England Temperature dataset) (independent variable) for 1990–99 (Meteorological Office, 2009c). The predicted air temperature increases were applied (+2 °C, +3 °C, +5 °C) to the CET data, using the regression outputs with their 95% confidence limits, and converted to R_T for the period 2050–59. For each temperature change prediction, this enabled calculation of the predicted number of days above a series of threshold temperatures, allowing comparison with the thermal requirements of the non-native fishes using values obtained from literature, primarily their thermal requirements for reproduction (e.g. Billard, 1999; Copp *et al*., 2009a).

Results

At least 38 species of non-native freshwater fish have been introduced to England and Wales, with 12 recorded in 10 waters or less and 6 recorded in more than 101 waters (Table 1). Fifteen of the 38 species have established at least one persistent, self-sustaining population, and there are 14 species for which evidence suggests they are no longer present in the wild (Table 1). Of the species present in more than 101 waters, five had FISK scores ≥19 (Table 1).

The effect of latitude on air temperature in England and Wales, after accounting for the effects of altitude,

Table 1 Non-native fishes introduced into England and Wales, the known decade of introduction into the wild, the type of introduction (S = intentional stocking, A = accidental, R = release of aquarium⁄pond specimens), the extent of occurrence (i.e. the number of sites where the species has been recorded: 0, 1, 1–10, 11–50, 51–100, >101), their current status (i.e. E = established self-sustaining population, N = not established, ? = possibly or no recent confirmation of past reports of establishment, Ex = extirpated) and FISK (Fish Invasiveness Scoring Kit) score (from Copp *et al.*, 2009a; * = G.H. Copp unpublished; '–' indicates that a score is not available

Scientific name	Common name	Decade	Type	Extent	Status	FISK
Cyprinus carpio L.	Common carp	1490s	S	>101	E	37.3*
Silurus glanis L.	European catfish	1860s	S	>101	E	21.5
Carassius auratus (L.)	Goldfish	1690s	S⁄R	>101	E	30.2
Leuciscus idus (L.)	Ide	1870s	S	>101	E	20.0*
Sander lucioperca (L.)	Pikeperch	1870s	S	>101	E	23.0
Oncorhynchus mykiss (Walbaum)	Rainbow trout	1880s	S	>101	E	19.3*
Ctenopharyngodon idella (Valenciennes)	Grass carp†	1960s	S	51–100	N	24.0
Lepomis gibbosus (L.)	Pumpkinseed	1900s	S	11–50	E	27.5
Leucaspius delineatus (Heckel)	Sunbleak	1980s	A	11–50	E	21.0
Pseudorasbora parva (Temminck & Schlegel)	Topmouth gudgeon	1980s	A	11–50	E	35.0
Rhodeus amarus (Bloch)	Bitterling	1920s	A⁄R	11–50	E	12.5
Acipenser ruthenus L.	Sterlet	1990s	S⁄R	11–50	N	16.0
Misgurnus mizolepis L.	Asian weatherfish	2000s	A⁄R	1–10	E	–
Pimephales promelas Rafinesque	Fathead minnow	1990s	A⁄R	1–10	E	19.0
Umbra krameri Walbaum	European mudminnow	1920s	A⁄R	1–10	N	11.0
Salvelinus fontinalis (Mitchell)	Brook trout	1860s	S	1–10	E	13.8
Ameiurus melas (Rafinesque)	Black bullhead	1920s	S	1–10	E	28.8
Ictalurus punctatus (Rafinesque)	Channel catfish	1920s	S	1–10	?	23.8
Hypophthalmichthys molitrix (Valenciennes)	Silver carp†	1980s	S	1–10	N	22.8
Hypophthalmichthys nobilis (Richardson)	Bighead carp†	1980s	S	1–10	N	24.3
Misgurnus fossilis (L.)	European weatherfish	1960s	A⁄R	1–10	E	12.5
Maylandia (*Metriaclima*) sp.	Zebrafishes‡	1950s	R	1	N	–
Ameiurus catus (L.)	White catfish	2000s	R	1	N	–
Catostomus commersonii (Lacepède)	White sucker	1980s	A	1	?	23.0
Acipenser baerii (Brandt)	Siberian sturgeon	1990s	S	0	N	18.0
Oncorhynchus gorbuscha (Walbaum)	Pink salmon	1960s	S	0	N	17.3
Salmo salar sebago L.	Landlocked salmon	1980s	S	0	N	10.0
Salvelinus namaycush (Walbaum)	American lake charr	1920s	S	0	N	27.5*
Cyprinella lutrensis (Baird & Girard)	Red shiner§	1980s	–	0	?	18.0
Poecilia reticulate (Peters)	Guppy¶	1960s	R	0	Ex	–
Channa micropeltes (Cuvier)	Giant snakehead‡	2000s	R	0	N	26.8
Clarias batrachus (L.)	Walking catfish‡	2000s	R	0	N	–
Coregonus clupeaformis (Mitchill)	Lake whitefish**	1880s	S	0	N	–
Hypostomus plecostomus L.	Suckermouth catfish††	2000s	R	0	N	–
Pygocentrus sp. (*nattereri*)	Piranha‡	2000s	R	0	N	–
Tilapia zillii (Gervais)	Redbelly tilapia‡‡	1960s	R	0	Ex	–
Ambloplites rupestris (Rafinesque)	Rock bass§§	1930s	S	0	N	13.0
Micropterus salmoides (Lacepède)	Largemouth bass§§	1880s	S	0	N	15.5

†Species classed as 'vagrants' because of their inability to establish in the British Isles, even under conditions of increased temperature, because of the absence of long, uninterrupted river courses; ‡Tropical species – single specimens found dead or nearly so (for *Pygocentrus* sp. [*nattereri*], see Ellis, 2006); §Semi-tropical species – some unconfirmed reports of the species in ornamental ponds in the London area (Parrott *et al.*, 2009); ¶Tropical species that established in heated outfall waters only and disappeared as soon as the discharges ceased, Gbut establishment of the species in Spain (Elvira and Almodovar, 2001) suggests establishment in southern England may be possible with increased temperature; **Failed to establish so stocking programme ceased; ††Live specimens found during summer months in Essex (K.J. Wesley, personal communication) and Leicestershire (London Metro, 2009); ‡‡Tropical species that established in heated outfall waters only and disappeared as soon as the discharges ceased (Wheeler & Maitland, 1973), and unlikely to establish in the British Isles; §§No firm evidence of the establishment of persistent, reproducing populations – the available information indicates that the remaining specimens have been extirpated either by natural or human agent (Copp *et al.*, 2007).

longitude and precipitation, was significant ($F_{2,43} = 14.1$, $P < 0.001$). Of the covariates, altitude and longitude also had significant effects ($F_{1,44} = 5.1$, $P < 0.05$; $F_{1,44} = 10.3$, $P < 0.05$, respectively). The pairwise comparisons with Bonferroni adjustments for multiple comparisons revealed the difference between Groups 1 and 2 was significant at 1.1 ± 0.32 °C ($P = 0.004$) and Groups 1 and 3 was significant at 1.99 ± 0.39 °C ($P < 0.001$). However, the difference between Groups 2 and 3 was not significant (mean 0.89 ± 0.44 °C, $P = 0.12$). Thus, the mean Climatch scores were obtained for the 24 non-native fishes present in England and Wales for Group 1, and for Groups 2 and 3 combined (hereafter referred to as Groups 2, 3).

The grouped air temperature data collected along the latitudinal gradient between 40 and 49 °N through France and Spain were tested against the air temperature data of the two latitudinal groups from England and Wales. When controlled for the effects of altitude, longitude and precipitation, the effect of latitude on temperature was significant (April: $F_{6,109} = 51.1$, $P < 0.001$; July: $F_{6,109} = 48.9$, $P < 0.001$; September: $F_{6,109} = 99.5$, $P < 0.001$, respectively). The effects of altitude were also significant for April ($F_{1,114} = 13.2$, $P < 0.001$) and July ($F_{1,114} = 27.1$, $P < 0.001$) but not September ($P > 0.05$). The effect of longitude was only significant in April ($F_{1,114} = 8.9$, $P < 0.01$), and the effect of precipitation was not significant in any month. Pairwise comparisons with Bonferroni adjustments for multiple comparisons of the mean differences in temperature between the months revealed that Group 1 was significantly different from Group 6 by between 2.3 and 2.7 °C and Groups 2, 3 was significantly different from Group 7 by between 2.5 and 2.9 °C (Table 2). As the differences between these groups were most similar to the climate change scenario for England and Wales in 2050 (minimum air temperature increase of +2 °C), Groups 6 and 7 were used as the Target regions for the predictive Climatch models for Groups 1 and 2, 3, respectively (Table 2).

Comparison of the Climatch output for 2009 for England and Wales with their predicted values in 2050 revealed that in Group 1 four species had mean Climatch scores that increased from <7.0 to >7.0, namely *Silurus glanis*, *Cyprinus carpio*, *Lepomis gibbosus* and *Carassius auratus* (Fig. 1a). In Groups 2, 3, the same species were also predicted to increase in this manner, as were also both *Rhodeus amarus* and *Pimephales promelas* (Fig. 1b). Regarding the predictions for the other species, five were predicted to have decreased temperature compatibility in both groups in 2050 (e.g. *Leuciscus idus* and *Leucaspius delineatus*) and six were predicted to increase but without exceeding a mean Climatch score of 7.0 (e.g. *Ictalurus punctatus* and *Hypophthalmichthys nobilis*; Fig. 1).

Of the six non-native species predicted to have increased temperature compatibility (mean score >7.0) between their native range and England and Wales in 2050 (Table 1; Fig. 1), *S. glanis* and *C. carpio* not only have relatively high FISK scores (21.5 and 37.3, respectively; Table 1), but also exert the highest levels of propagule pressure of all non-native fishes in England and Wales (Figs 2 & 3). This is mainly owing to their popularity with anglers, which results in their regular stocking into lacustrine fisheries (generally <5 ha). For example, over six million *C. carpio* were

Table 2 Mean differences, indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons in each GLM (general linear model), for air temperatures in England and Wales (Groups 1 and 2, 3) and France and Spain (Groups 4 to 8) after removing the effects of altitude, longitude and precipitation. In the table, the groups highlighted by grey shading were those with the closest match to the predicted thermal conditions of Groups 1 and 2, 3 in England and Wales in 2050

Mean difference between groups (±SE) (°C)				
	Latitude (°N)	April	July	September
Group 1 (*n* = 16) 50–51				
Group 4 (*n* = 15)	40–41	5.1 ± 0.8	6.9 ± 0.8	6.9 ± 0.5
Group 5 (*n* = 15)	42–43	3.4 ± 0.3	4.4 ± 0.4	4.6 ± 0.3
Group 6 (*n* = 15)	44–45	2.3 ± 0.4	2.7 ± 0.5	2.3 ± 0.4
Group 7 (*n* = 14)	46–47	1.2 ± 0.3*	1.4 ± 0.4**	1.6 ± 0.3
Group 8 (*n* = 11)	48–49	0.7 ± 0.4***	0.3 ± 0.5***	0.7 ± 0.4***
Groups 2, 3 (*n* = 29) 52–55				
Group 4 (*n* = 15)	40–41	6.6 ± 0.6	8.6 ± 0.8	8.4 ± 0.5
Group 5 (*n* = 15)	42–43	4.9 ± 0.3	6.1 ± 0.4	6.1 ± 0.3
Group 6 (*n* = 15)	44–45	4.1 ± 0.4	5.0 ± 0.5	4.5 ± 0.4
Group 7 (*n* = 14)	46–47	2.5 ± 0.3	2.8 ± 0.4	2.9 ± 0.3
Group 8 (*n* = 11)	48–49	2.1 ± 0.4	1.8 ± 0.5	1.7 ± 0.3

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

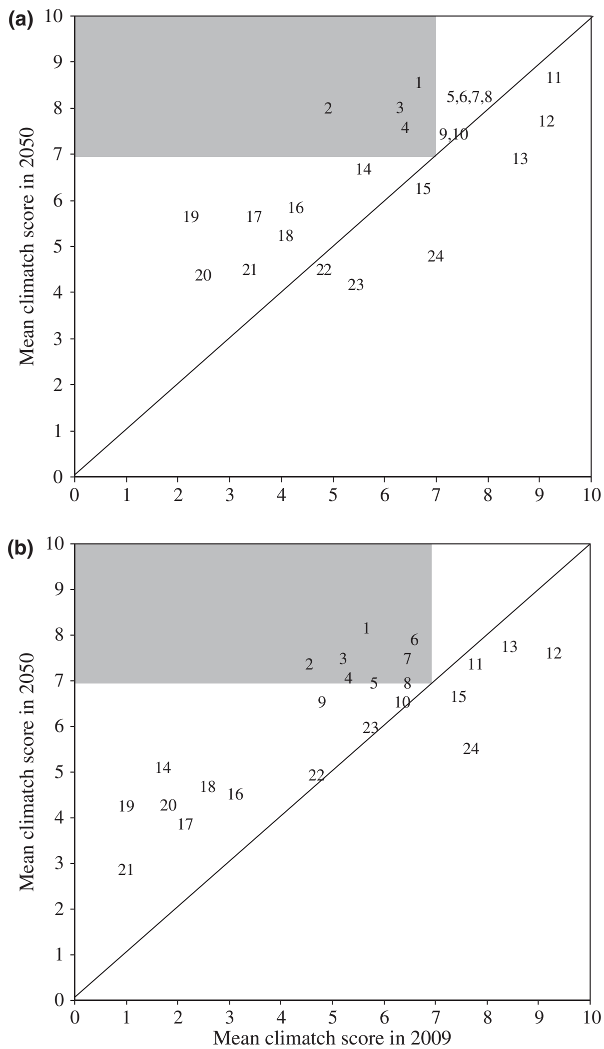

Fig. 1 Comparison of mean Climatch scores between 2009 and 2050 for 24 non-native fishes present in England and Wales where (a) comparison for species in Group 1 (50–51°N) and (b) comparison for species in Group 2, 3 (52–55°N). On each graph, the solid line represents the 45° line; species with scores above this line have an increased climate match with the Source region in 2050 when compared with 2009. Species scores that lie within the grey box are those whose climate match in 2009 was below 7.0, but above 7.0 in 2050. Species key: 1 *Silurus glanis*; 2 *Cyprinus carpio*; 3 *Lepomis gibbosus*; 4 *Carassius auratus*; 5 *Pseudorasbora parva*; 6 *Rhodeus amarus*; 7 *Pimephales promelas*; 8 *Umbra krameri*; 9 *Misgurnus mizolepis*; 10 *Misgurnus fossilis*; 11 *Leucaspius delineatus*; 12 *Leuciscus idus*; 13 *Sander lucioperca*; 14 *Ameiurus melas*; 15 *Oncorhynchus mykiss*; 16 *Ictalurus punctatus*; 17 *Ameiurus catus*; 18 *Maylandia* spp.; 19 *Hypophthalmichthys nobilis*; 20 *Ctenopharyngodon idella*; 21 *Hypophthalmichthys molitrix*; 22 *Acipenser ruthenus*; 23 *Catostomus commersonii*; 24 *Salvelinus fontinalis*.

consented for stocking into lakes in England and Wales between 1998 and 2008, with at least 1.54 million consented for release into lakes that provide potential for their natural dispersal (Figs 2 & 3). Although data are less precise for *S. glanis* introductions, specimens have been released into at least 250 recreational lake fisheries, the majority of which have occurred in recent years, with the largest stocked fish being approximately 27 kg (Fig. 2; Clarke, 2005). Correspondingly, these two species have also been increasingly recorded in rivers because of their dispersal from floodplain waterbodies (Fig. 2), with *C. carpio* recorded during Environment Agency river fishery monitoring surveys on 1224 occasions between 1980 and 2008. Indeed, there was a significant increase in the annual number of riverine sites where carp were recorded in the period ($r^2 = 0.65$, $F_{1,27} = 50.3$, $P < 0.001$; Fig. 3).

In the light of the indications (data from climate-matching, spatial distribution and propagule pressure) that *C. carpio* and *S. glanis* are the species likely to benefit most from climate warming in England and Wales, this prediction was then tested using water temperature modelling. The relationship between CET and R_T from 1990 to 1999 was described by $R_T = (0.95 \times \text{CET}) + 2.97$ ($r^2 = 0.84$, $F_{1,3651} = 14684.2$, $P < 0.001$). Lower 95% confidence limits were $R_T = (0.93 \times \text{CET}) + 2.79$ and higher $R_T = (0.97 \times \text{CET}) + 3.14$. When used to predict R_T between 2050 and 2059, outputs suggested that with a mean air temperature increase of 2 °C, there will be sufficient degree-days >20 °C every year for at least a single spawning event for *C. carpio* (1200 degree-days >20 °C; Billard, 1999), with multiple spawning events then possible at increases of 3 and 5 °C (Fig. 4). For *S. glanis*, reproduction may remain slightly constrained with a 2 °C mean air temperature increase, but increases of either 3 and 5 °C will enhance their ability to reproduce regularly because of the occurrence of temperatures >22 °C over prolonged periods of time, i.e. their minimum thermal requirements for spawning (Copp *et al*., 2009a, 2009b; Fig. 4).

Discussion

Warmer temperatures because of the climate change are predicted to favour the establishment of a low number of non-native fishes in England and Wales, enhancing their likelihood of becoming invasive. Owing to their current distribution and propagule pressure, most notable amongst these are *C. carpio* and *S. glanis*. The FISK outputs suggest that substantial

Fig. 2 Locations of introduced *Silurus glanis* in connected and floodplain lakes in England and Wales (▲); locations of recordings of *S. glanis* in rivers in England and Wales (Δ); locations of stockings of *Cyprinus carpio* into lakes in the floodplain in England and Wales 1998–2008 (●); recordings of *C. carpio* in rivers in England and Wales 1980–2008 (■).

ecological impacts may result should *C. carpio* develop invasive populations in England and Wales, and although *S. glanis* is predicted to be less invasive (Copp *et al.*, 2009a), potential impacts may be accentuated by other human-mediated environmental changes such as river impoundment (Copp *et al.*, 2009b). In favourable thermal conditions, *C. carpio* are capable of rapid growth and have a high reproductive capacity involving multiple spawning strategies (Vilizzi, 1998; Smith & Walker, 2004), leading to impacts such as detrimental effects through interspecific competition and the displacement of native fishes (Koehn, 2004). A bio-engineering species, *C. carpio* is a vigorous benthic feeder whose foraging behaviour results in declines in submerged vegetation directly through uprooting or herbivory and indirectly through bioturbation and excretion (Williams, Moss & Eaton, 2002; Britton *et al.*, 2007). The species also induces the resuspension of sediments that could change water transparency from clear to turbid (e.g. Crivelli, 1983; Lougheed, Crosbie & Chow-Fraser, 1998; Parkos, Santucci & Wahl, 2003; Koehn, 2004; Lougheed *et al.*, 2004; Matsuzaki *et al.*, 2007, 2009a). The threat of *C. carpio* is enhanced by its ability to adapt rapidly from domestic to feral forms, resulting in a more streamlined body shape and higher consumption rates because of greater prey detection and capture relative to the domestic form (Matsuzaki *et al.*, 2009a,b).

By comparison, evidence of ecological impacts of non-native *S. glanis* elsewhere in their introduced range is less clear (Copp *et al.*, 2009b). In Iberia, where *S. glanis* was introduced in the 1970s and is now well established, individual fish achieve body weights >100 kg (Elvira & Almodovar, 2001; Carol, Zamora & García-Berthou, 2007) and those >1.2 m in length prey upon fish of up to 50 cm (2 kg) and water birds (Carol *et al.*, 2009). The large body and gape sizes that the species can achieve also mean that it can potentially predate on species and/or individuals that would otherwise have reached a size-refuge from predation. For instance, in France, Syväranta *et al.* (2009) demonstrated a significant contribution of anadromous species to the diet of *S. glanis*, averaging 53–65% in some cases. However, a thorough review of the literature indicates that *S. glanis* is more of an opportunistic scavenger than a voracious predator (Copp *et al.*, 2009b). Moreover, ecological impacts of non-native aquatic species are notoriously difficult to predict because of concomitant changes in biological interactions that will also occur through warming

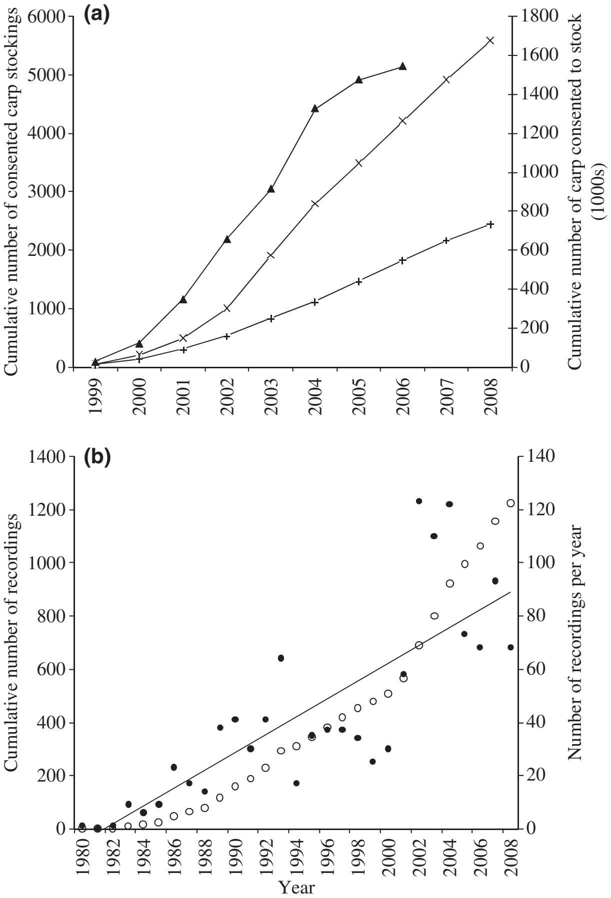

Fig. 3 (a) Cumulative number of consented *Cyprinus carpio* stockings into open waters (connected and floodplain lakes) (×), cumulative number of *C. carpio* stockings into open waters (connected and floodplain lakes) where there was no previous electronic record of their presence (+), and the cumulative number of *C. carpio* stocked into open waters (▲). All data are for 1999–2008. (b) Total number of recordings of *C. carpio* in rivers in England and Wales for 1980–2008 (o) and the number of recordings of *C. carpio* per year in rivers in England and Wales for 1980–2008 (●) and their temporal trend (linear regression, solid line, r^2 = 0.65, $F_{1,27}$ = 50.3, P < 0.0001).

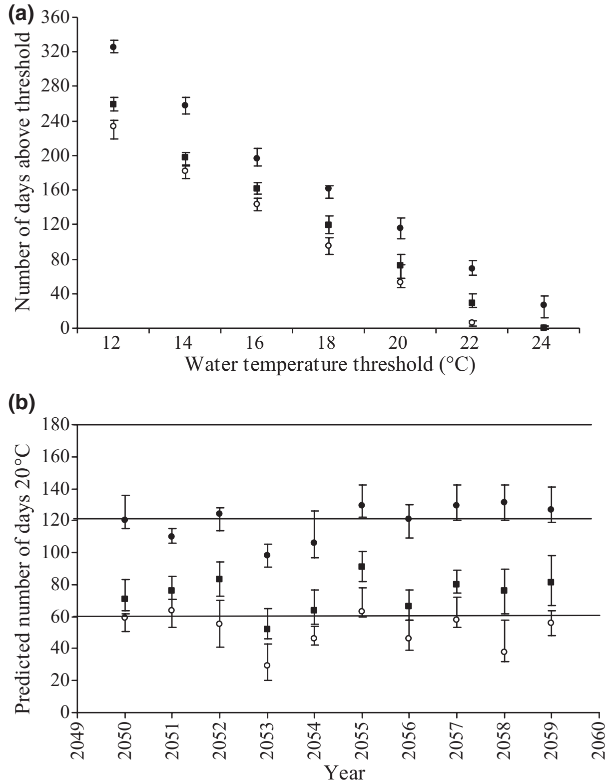

Fig. 4 (a) Predicted number of days above a range of water temperature thresholds in the River Trent for a year of mean air temperatures in the 2050s. (b) Predicted number of days >20 °C in the River Trent between 2050 and 2059; horizontal lines denote periods of 1200 degree-days >20 °C necessary for maturation of *Cyprinus carpio* ovaries (Billard, 1999). Key: o: predicted air temperature +2 °C;■: +3 °C ●: +5 °C; error bars represent values derived from the 95% confidence limits calculated in the linear regression calculation.

temperatures, for example in the competitive ability and predator–prey relationships between the native fishes, and between the native and introduced fishes (Rahel & Olden, 2008).

Although a crucial factor in determining establishment success, water temperature is not the only factor influencing the establishment and invasion of non-native fishes in England and Wales. Such effects of climate change are likely to be more complex, potentially involving interrelated changes in precipitation patterns, river hydrology, water chemistry and riparian and in-stream flora (e.g. Johnson *et al*., 2009). Interactions between the non-native and native species will be important, especially as some native cold-water species will reduce in their spatial distribution because of the warming temperatures, irrespective of introduced fishes (Buisson *et al*., 2008). The role of habitat quality, geomorphology and catchment land use will also be important consideration (Holway & Saurez, 1999; Ross *et al*., 2001; Garcia-Berthou *et al*., 2005; Vila-Gispert, Alcaraz & Garcia-Berthou, 2005). For example, the climate modelling predicted that the establishment and invasion of *L. gibbosus* in England and Wales would be enhanced by increased temperatures. In conjunction with greater hydrological variability, their reproduction is likely to be favoured within water courses (Copp & Fox, 2007). However, their range expansion into new river catchments via translocation remains unlikely because of low propagule pressure (i.e. minimal angling interest, an absence of commercial consignments) and legislative controls. This contrasts to *C. carpio* and *S. glanis*, which indicate that even relatively small increases in water temperature are likely to enhance their ability to establish and become invasive, especially as this will be facilitated by their high levels of propagule pressure.

Irrespective of the potential ecological consequences of allowing *C. carpio* to obtain a wide distribution in England and Wales, this must be measured against the ecosystem services they support. In Australia and North America, *C. carpio* is considered a pest (e.g. Lougheed *et al*., 1998; Koehn, 2004), but in considerable portions of Europe, Asia and Africa they are a food fish (e.g. Britton *et al*., 2007). Moreover, in England and Wales, *C. carpio* is the key species in a catch-and-release recreational angling industry worth £3 billion per annum (Environment Agency, 2004). As *C. carpio* is considered as 'ordinarily resident' (primarily as it has been present for so long), the species is effectively ignored by national legislation on non-native species and is treated by regulatory authorities in a similar manner to native fishes (Copp *et al*., 2009a). For instance, in the review article by Hickley & Chare (2004) on non-native fisheries in England and Wales, *C. carpio* is not listed amongst the four case studies on non-native species that concern coarse fisheries but rather as the species most preferred by coarse fish anglers. Hence, stocking of *C. carpio* remains a widespread means of enhancing recreational fisheries (Britton *et al*., 2005). Notwithstanding, the ecological cost of allowing *C. carpio* obtain such a wide, uncontrolled distribution may only be determined in years to come.

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