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## Heated competition: how climate change will affect non-native pumpkinseed *Lepomis gibbosus* and native perch *Perca fluviatilis* interactions in the U.K.

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Heated and ambient temperature experimental ponds were used to examine competition between introduced pumpkinseed *Lepomis gibbosus* and native perch *Perca fluviatilis* in England, U.K., and how these interactions are likely to change under climate warming conditions. Results from three sets of two-week experiments indicated that in both species and in all sets, growth was faster in heated than in ambient temperature ponds. Growth of both *P. fluviatilis* and *L. gibbosus* in sympatry did not differ significantly from that observed in allopatric ponds. Diet analysis indicated that increased resource partitioning occurred when *P. fluviatilis* and *L. gibbosus* were reared in sympatry, with *P. fluviatilis* shifting to a diet higher in microcrustaceans. The results do not support the previous claims of adverse effects of *L. gibbosus* on *P. fluviatilis* populations. Under conditions of climate change, however, which have been demonstrated experimentally to enhance *L. gibbosus* recruitment, this species is expected to become invasive in England, resulting in higher densities that may exert a stronger competitive effect than examined in this study.

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Key words: growth; interspecific competition; invasive species; temperature.

### INTRODUCTION

Global climate change is expected to incite shifts in community structure in both marine and freshwater systems, posing a threat to the stability and function of aquatic ecosystems. Warming temperatures should increasingly favour warm-water species (Soto, 2001; Daufresne *et al.*, 2003; Dembski *et al.*, 2008; Graham & Harrod, 2009), and the effects of climate change on biological and ecological processes are predicted to affect the distribution, abundance and impact of non-native aquatic species. These changes will probably alter the pool of potential invaders, facilitate invasions by some currently non-invasive species, and increase the impact of some established invasive species (Hellmann *et al.*, 2008; Rahel & Olden, 2008; Graham & Harrod, 2009).

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The warm-water North American pumpkinseed *Lepomis gibbosus* (L. 1758) is one of six introduced fish species in the U.K. expected to benefit from climate warming (Britton *et al.*, 2010). Introduced to Europe during the late 19th century, *L. gibbosus* now has established populations in at least 28 countries of Europe and Asia Minor and is considered one of the most successful introduced fishes in Europe (Holčík, 1991; Copp & Fox, 2007). The invasive success of *L. gibbosus* is greatest in the southern regions of its non-native distribution, in particular in the Iberian Peninsula, where its rapid spread in recent decades has coincided with adverse interactions with some indigenous species (Zapata & Granado-Lorencio, 1993; Godinho & Ferreira, 1998; Gutiérrez-Estrada *et al.*, 2000). Throughout most of its southern (*i.e.* warmer) distribution *L. gibbosus* is considered invasive but it is classified as non-invasive in most of its northerly range, including the U.K., where it has been present in southern England for over a century (Cucherousset *et al.*, 2009), as there is no evidence of any adverse effects on native taxa or ecosystem function.

Shortly after its introduction to Europe, *L. gibbosus* was quickly labelled a pest species (Künstler, 1908), and was subsequently blamed for declines in native perch *Perca fluviatilis* L. 1758 (Roule, 1931), although these latter claims have never been tested and evidence for this is lacking. The potential for competition between these two species is high, as both *P. fluviatilis* and *L. gibbosus* are well known to be associated with the littoral zone, and at certain life stages share a preferred diet of macroinvertebrates (Scott & Crossman, 1973; Hanson & Leggett, 1986). In its native range, *L. gibbosus* has been linked to reduced growth and sub-optimal diet shifts in yellow perch *Perca flavescens* (Mitchill 1814) (Hanson & Leggett, 1985, 1986), which is functionally similar to *P. fluviatilis* (Thorpe, 1977). In its introduced range, *L. gibbosus* populations are known to demonstrate relatively faster juvenile growth and earlier maturation in the southern, warmer parts of Europe than in the native and introduced cool-water populations (Villeneuve *et al.*, 2005; Copp & Fox, 2007). It is therefore hypothesized that *L. gibbosus* would have a competitive advantage over *P. fluviatilis*, particularly in a heated environment, which would be manifested as reduced growth of, and reduced quantity and quality of food consumed by *P. fluviatilis* when reared in sympatry with *L. gibbosus*. The aim of this study was to test this hypothesis using ambient temperature and heated experimental ponds to examine the competitive interactions between introduced *L. gibbosus* and native *P. fluviatilis* in England, and to determine how these interactions are likely to change under increased temperatures predicted by current climate change models. Specifically, the objectives of the study are to determine the effects of temperature and competition on the: (1) growth rate, (2) quantity of food consumption and (3) quality of diet of *L. gibbosus* and *P. fluviatilis*. This study has particular relevance to potential climate change effects on European inland waters (Dembski *et al.*, 2006; Masson *et al.*, 2008), with reference to the response and interactions of existing non-native fish species with native species and ecosystems (Britton *et al.*, 2010; Zięba *et al.*, 2010).

## MATERIALS AND METHODS

The existence of competition between *P. fluviatilis* and non-native *L. gibbosus* was tested by experimentally manipulating species combinations and temperature in six artificial ponds,

located at Tanyard Fisheries in East Sussex, England ( $51^{\circ} 01' 07''$  N;  $00^{\circ} 00' 47''$  E), in the River Ouse (Sussex) catchment where many of the introduced *L. gibbosus* populations in the U.K. are found (Villeneuve *et al.*, 2005). Each  $5\text{ m} \times 5\text{ m}$  pond had a maximum depth of c. 1.2 m, and was fitted with a water recirculation system (P2500 fountain pump, Blagdon; [www.blagdonwatergardens.co.uk](http://www.blagdonwatergardens.co.uk)), which pumped water from the pond into a fibreglass cistern ( $0.2\text{ m}^3$ ) at a maximum rate of  $2400\text{ l h}^{-1}$ . Water was then returned to the pond through an overflow pipe. Three of the ponds were maintained at ambient temperature and three were artificially heated using 750 W Velda floating styrofoam heaters ([www.velda.com](http://www.velda.com)), located in the fibreglass cisterns, to maintain heated ponds at c.  $2\text{--}3^{\circ}\text{C}$  above ambient in line with climate change predictions (Hulme *et al.*, 2002). Water temperature was monitored using Tiny-Tag Aquatic 2 temperature loggers (Gemini Data Loggers Ltd; [www.gemindataloggers.com](http://www.gemindataloggers.com)). Two of the six ponds (one ambient and one heated) were used as holding units for fishes prior to their use in experiments, with each pond separated into two compartments (one for each species) by a plastic mesh barrier. To support benthic invertebrates, c. 8 cm of silt-clay soil was added to each pond in early May to cover the plastic-lined bottom. Netting was fixed over the surface of each pond to deter avian and mammalian predators.

Four sets of experiments, each of 14 days duration, were undertaken from 3 June to 18 August 2010 under licence from the U.K. Home Office, accompanied by the necessary consents and derogations as regards the Import of Live Fish (England and Wales) Act 1980 and related legislation. The first set was conducted when available prey were not yet well established, as indicated by low macroinvertebrate density (means based on benthic core sampling were 25–40% of those of the other three sets) and the negative change in body mass of many fishes; it was therefore excluded from the analyses.

*Perca fluviatilis* used in the experiments were collected by seine from a pond near Hatfield, Hertfordshire ( $51^{\circ} 46'$  N;  $13^{\circ} 13'$  W). Individuals varied in total length ( $L_T$ ) from 75 to 160 mm, with most between 80 and 110 mm, a size range most likely to compete with *L. gibbosus* for food sources in the littoral zone (Horppila *et al.*, 2000). *Lepomis gibbosus* were caught by electrofishing from adjacent ponds in Tanyard Fisheries;  $L_T$  ranged from 68 to 132 mm. Following capture, fishes were transferred to holding tanks in the fishery, where they were individually tagged under anaesthesia (*L. gibbosus*, as described by Stakėnas *et al.*, 2009; *P. fluviatilis*, using clove oil at  $40\text{ ml l}^{-1}$ ), with  $2\text{ mm} \times 12\text{ mm}$  passive integrated transponder (PIT; [www.wyremicrodesign.co.uk](http://www.wyremicrodesign.co.uk)) tags, and allowed to recover fully in tanks before transfer to holding ponds, where they were placed at least 2 weeks prior to their use in the experiments in order to acclimatize to the appropriate pond temperature.

At the beginning of each set of experiments, each of the four experimental ponds was stocked with c. 320 g biomass of fishes (mean  $\pm$  S.E.  $12.6 \pm 2.1\text{ g m}^{-2}$ ); a biomass equivalent to the medium density treatment used by Hanson & Leggett (1985) in their *P. flavescens* and *L. gibbosus* enclosure experiments. Ponds were stocked with one of the three species assemblages: *P. fluviatilis* alone (allopatric), *L. gibbosus* alone (allopatric), or the two species together with 50% of the biomass provided by each species (sympatric). There were a total of six treatments (three species combinations at two pond temperatures). In all sets, mixed-species assemblages were assessed in both ambient and heated ponds, while single-species assemblages were alternatively assigned to either ambient or heated ponds. Treatments were initially assigned to a pond at random. In subsequent sets, a different species assemblage was assigned to each pond to limit the effect of among-pond variation on a particular species assemblage. Test fishes were weighed to the nearest 0.01 g (wet mass) and measured for  $L_T$  (nearest mm) at the start of each set, and again at the end of the two-week period immediately following removal from the ponds. A total of 274 *P. fluviatilis* and 134 *L. gibbosus* were used in the experiments.

Ponds were monitored and serviced daily; floating debris (*e.g.* leaves) was removed from the surface, pumps were cleaned and visible mortalities were removed. Benthic invertebrate samples were collected at the beginning and end of each set (*i.e.* every 2 weeks) from each pond using a  $33.2\text{ cm}^2$  plexiglas core sampler to monitor prey densities over the course of the experiments. Samples were washed through 500 and  $106\text{ }\mu\text{m}$  mesh Tyler sieves. Organisms were picked by hand from the sieves and identified to order or family and counted.

On the morning of day 15, the anti-bird nets were removed from the ponds and all test fishes were collected by seining, killed with an overdose of 2-phenoxyethanol and chilled to

freezing, with storage in labelled plastic bags. On average, two seines per pond were required to remove all fishes, and complete removal of fishes from the four experimental ponds took  $\leq 2$  h.

In the laboratory, the stomach contents of a randomly selected sub-sample of eight to 10 fish per treatment and experimental run were examined; a total of 120 *P. fluviatilis* and 103 *L. gibbosus* stomachs were used in the diet analysis. The diets of fishes in each experimental treatment were determined by examining the stomach contents under a dissecting microscope. The number and volume of each prey type was estimated visually with the aid of a Petri dish grid, and invertebrates were classified into one of the 13 prey groups: microcrustaceans (includes *Daphnia* spp., *Chydorus* spp., *Alona* spp., Ostracoda), Araneae (specifically *Argyroneta* spp.), Chironomidae, Coleoptera, Corixidae, Culicidae, Ephemeroptera, Gastropoda, Hemiptera (other than Corixidae), Simuliidae, adult insects, fishes and others. Prey types that made up  $<0.5\%$  of the mean volume in both *P. fluviatilis* and *L. gibbosus* diets were grouped as other, which included Anisoptera, Ceratopogonidae, Hydrachnidiae, Plecoptera, Trichoptera, Tubificidae (*Tubifex* spp.), Zygoptera and plant material. The relative importance of each prey type in the diet was calculated as their percentage (by volume) of all prey eaten by fishes in the population in question on the day of harvest. The diet of *P. fluviatilis* and *L. gibbosus* of the size ranges used in this study normally consists primarily of macroinvertebrates; microcrustaceans are preyed upon by both species during earlier life stages, but only occasionally and in small quantities once they are large enough to feed on macroinvertebrates of greater energetic value (Guma'a, 1978; Hanson & Leggett, 1986; Fox & Keast, 1990; Godinho *et al.*, 1997). For this reason, microcrustaceans were considered *a priori* as an energetically inferior food source in the ponds.

## DATA ANALYSIS

To assess seasonal changes in benthic invertebrate abundance in the experimental ponds, replicate samples taken from the four ponds during a set of experiments were pooled to obtain a single mean, and relative benthic invertebrate density (number of invertebrates  $m^{-2}$ ) was calculated. A one-way ANOVA was used to test for differences in benthic invertebrate availability across sets.

Instantaneous growth rate ( $G$ ) during a 2 week (14 days,  $t$ ) set was calculated for each fish [ $G = 100 \ln(M_{\text{final}} - M_{\text{initial}}) t^{-1}$ , where  $M$  = mass] and was used in treatment comparisons. Body size is a known endogenous factor affecting fish growth rate, and specific growth rate typically declines with body size (Wootton, 1998). Therefore, a linear regression was used to examine the relationship between initial  $L_T$  and  $G$  of both *P. fluviatilis* and *L. gibbosus*, and to examine the relationship between initial  $L_T$  and stomach fullness of both species. As expected, there was a negative relationship between *P. fluviatilis* initial  $L_T$  and  $G$  ( $F_{1,246} = 6.33$ ,  $P < 0.05$ ,  $r = -0.159$ ). Although the relationship between *L. gibbosus* initial  $L_T$  and  $G$  was not significant ( $F_{1,128} = 0.72$ ,  $P > 0.05$ ,  $r = -0.077$ ), initial  $L_T$  was used as a covariate in all statistical analyses of fish growth to account for the effect of fish body size on growth in experiments. The initial  $L_T$  of both *P. fluviatilis* and *L. gibbosus* was also inversely related to stomach fullness (*P. fluviatilis*:  $F_{1,108} = 16.04$ ,  $P < 0.001$ ,  $r = -0.36$ ; *L. gibbosus*:  $F_{1,96} = 21.37$ ,  $P < 0.001$ ,  $r = -0.43$ ), and therefore initial  $L_T$  was also used as a covariate in all statistical analyses of stomach fullness.

A fixed-effects general linear model was used for data analysis with  $G$  of *P. fluviatilis* and *L. gibbosus* as the dependent variables. The main factors were: experimental set, species assemblage (sympatric *v.* allopatric) and temperature treatment (heated *v.* ambient). The interactions between species assemblage and temperature treatment, and this interaction nested within the experimental set, were two additional factors included in the model. All comparisons of group means *via* the Fisher least-significant-difference (LSD) test were based on adjusted means for the initial  $L_T$  covariate. Reporting differences from Fisher's LSD test incorporated 95% C.I. as well as significance testing.

A fixed-effects general linear model was also used for data analysis with stomach fullness of *P. fluviatilis* and *L. gibbosus*, expressed as a percentage of total fish wet mass, as the dependent variables. Independent variables and statistical procedures were the same as those

used in the growth analysis. Significance was based on  $P < 0.05$ . Analyses were conducted in Statistica 10 (Statsoft; www.statsoft.com).

Spearman rank-order correlation was used to determine if there was a significant relationship between the relative volume of dominant prey types consumed by *P. fluviatilis* and *L. gibbosus* and individual fish  $G$ , as relative prey volumes were not normally distributed (Lilliefors test,  $P < 0.01$ ). The dietary overlap between *L. gibbosus* and *P. fluviatilis* was quantified using Schoener's similarity index, to identify dietary shifts under different experimental treatments (*i.e.* heated *v.* ambient, allopatric *v.* sympatric). Values  $\geq 0.6$  are considered to indicate significant diet overlap (Zaret & Rand, 1971). Specimens of *P. fluviatilis* and *L. gibbosus* were each divided into two size classes, based on the range of sizes used in the experiment, and Schoener's index was also used to identify differences in diet between the smaller and larger size classes of *P. fluviatilis* and *L. gibbosus*.

## RESULTS

The mean daily water temperature in the heated ponds was  $2.2 \pm 0.1^\circ \text{C}$  (mean  $\pm$  s.e.) higher than ambient pond temperatures (Fig. 1). The lowest recorded mean daily water temperatures were  $13.8$  and  $16.5^\circ \text{C}$ , for ambient and heated ponds, respectively (20 June), and the highest were  $22.2$  and  $25.1^\circ \text{C}$  (10 July).

Benthic invertebrate densities were significantly lower across all ponds in the first trial in comparison to the three subsequent sets, which supported the decision to exclude the trial from analysis ( $F_{3,52} = 5.99$ ,  $P < 0.01$ ; Fig. 2). Mean invertebrate densities in the ponds decreased from set 1 to set 3; however, these differences were not significant. The dominant macroinvertebrates in the benthic samples were Chironomidae ( $>90\%$ ).

Over the three sets of experiments, 8.8% of *P. fluviatilis* and 1.9% of *L. gibbosus* were not recovered from the ponds. Assuming that these were mortalities, mostly due

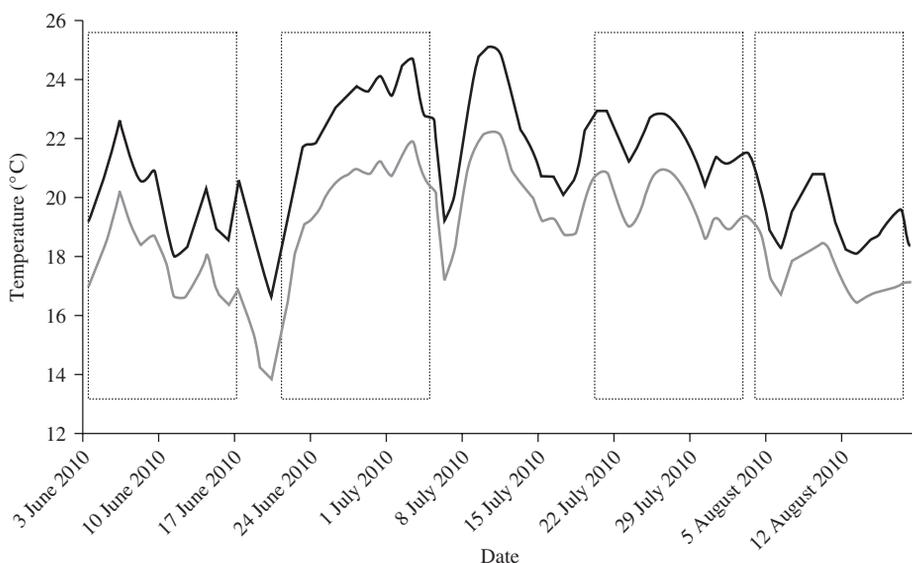


FIG. 1. Daily mean water temperatures in (—) ambient and (---) heated ponds during the study (3 June to 17 August 2010). □, periods when experiments were run.

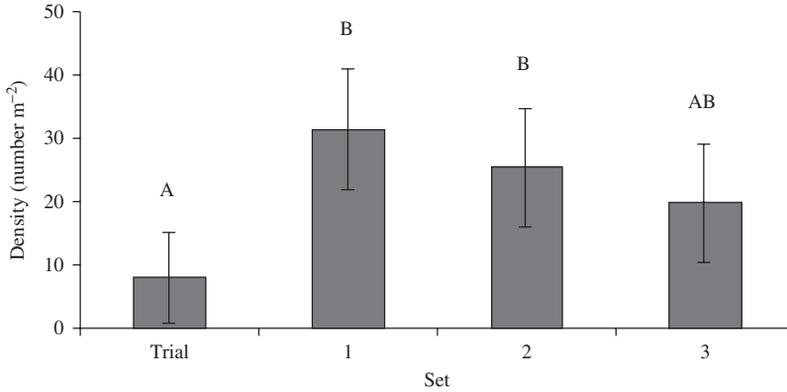


FIG. 2. Benthic invertebrate mean  $\pm$  95% C.I. relative densities across all ponds in each set. Means with different upper case letters are significantly different ( $P < 0.05$ ).

to handling and tagging stress and a few lost to avian predation, the mean mortality rate of *P. fluviatilis* was 10.5% in allopatric ponds and 8.1% in sympatric ponds. The mean mortality rate of *L. gibbosus* was 4.8% in allopatric ponds. There were no *L. gibbosus* mortalities in sympatric ponds.

The full models for *P. fluviatilis* and *L. gibbosus* were significant for both species in accounting for variation in *G* (*P. fluviatilis* full model,  $F_{3,158} = 7.55$ ,  $P < 0.001$ ; *L. gibbosus* full model,  $F_{3,92} = 8.58$ ,  $P < 0.001$ ; Table I). The analysis of *G* based

TABLE I. ANCOVA for the effects of initial total length ( $L_T$ ), set, species assemblage (allopatric *v.* sympatric) and temperature treatments (ambient *v.* heated) on the instantaneous growth rate of *Perca fluviatilis* and *Lepomis gibbosus*

Source of variation	d.f.	<i>F</i>	<i>P</i>
<i>P. fluviatilis</i>			
Intercept	1	35.25	<0.001
$L_T$	1	18.45	<0.001
Set	2	12.16	<0.001
Assemblage	1	0.24	>0.05
Temperature	1	108.21	<0.001
Assemblage $\times$ temperature	1	3.98	<0.05
Assemblage $\times$ temperature (set)	3	7.55	<0.001
Error	158		
<i>L. gibbosus</i>			
Intercept	1	52.72	<0.001
$L_T$	1	13.58	<0.001
Set	2	27.05	<0.001
Assemblage	1	6.19	<0.05
Temperature	1	9.64	<0.010
Assemblage $\times$ temperature	1	23.47	<0.001
Assemblage $\times$ temperature (set)	3	8.58	<0.001
Error	92		

on adjustment for the covariate, initial  $L_T$ , was an important contribution (*P. fluviatilis*  $L_T$  covariate,  $F = 18.45$ ,  $P < 0.01$ ; *L. gibbosus*  $L_T$  covariate,  $F = 13.58$ ,  $P < 0.01$ ).

The weakest contributions to the full model were attributable to the assemblage treatment (allopatric *v.* sympatric) for *P. fluviatilis* and *L. gibbosus*. For *P. fluviatilis*, there were no significant differences in  $G$  for individuals reared in allopatry or in sympatry with *L. gibbosus* (assemblage treatment) at ambient temperatures. For the heated treatment in set 2, *P. fluviatilis*  $G$  was 0.80% higher on a daily basis for individuals reared in allopatry relative to those reared in sympatry (mean difference, Fisher LSD,  $P < 0.01$ ). For allopatric *L. gibbosus*, the heated treatment in set 1 resulted in  $G$  being 1.73% lower on a daily basis when reared with *P. fluviatilis* than when reared in sympatry (mean difference, Fisher LSD,  $P < 0.01$ ). The  $G$  for allopatric *L. gibbosus* was effectively 0 (Fig. 3), indicating that there may still have been insufficient prey for fish in set 1.

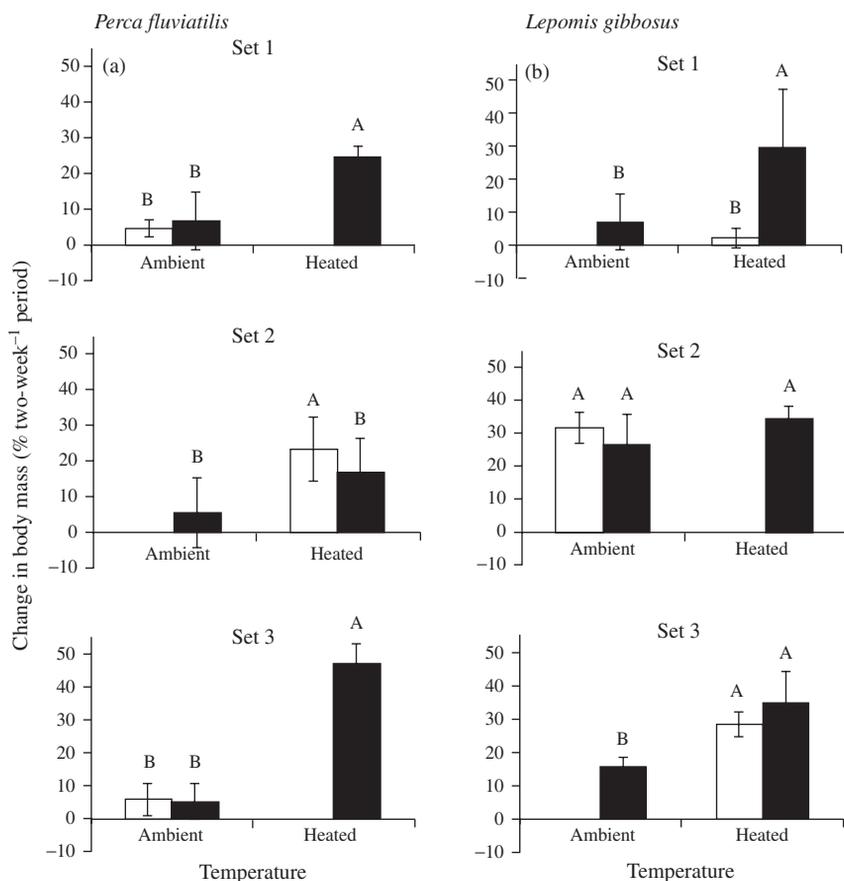


FIG. 3. Instantaneous growth rate (scaled in the figure as per cent body mass over the two-week period) of (a) *Perca fluviatilis* and (b) *Lepomis gibbosus* in (□) allopatric and (■) sympatric assemblages, in ambient and heated ponds. Values are mean  $\pm$  95% c.i.. Means with different upper case letters within species and set are significantly different ( $P < 0.05$ ).

Heated treatments resulted in higher  $G$  for both species within each set. The magnitude of this advantage differed between species depending on set. For both *P. fluviatilis* and *L. gibbosus* in set 2, individuals reared in the heated treatment did not show a significant increase in  $G$  relative to the ambient temperature treatment (both species mean difference = 0.5%, Fisher LSD test,  $P > 0.05$ ). For *P. fluviatilis*, the heated treatment resulted in significantly higher  $G$  in sets 1 and 3 over ambient treatment, with the greatest difference occurring in set 3 (mean difference = 2.19%, Fisher LSD test,  $P < 0.01$ ). For *L. gibbosus*, the heated treatment resulted in significantly higher  $G$  (Fisher LSD test,  $P < 0.01$ ) in sets 1 and 3 over ambient treatment, with the greatest difference occurring in set 1 (mean difference = 1.31%).

In *P. fluviatilis* sampled for diet analysis, 95% had food in their stomachs. *Perca fluviatilis* in sympatric treatments had 2.5 times the number of empty stomachs as those in allopatric treatments, and in heated conditions had twice the number of empty stomachs as those held in ambient conditions (Table II). In *L. gibbosus* sampled, 97% had food in their stomachs, and there was almost no difference in the percentage of empty stomachs neither between those reared in ambient and heated conditions, nor between those reared in the presence or absence of *P. fluviatilis*.

The full models for *P. fluviatilis* and *L. gibbosus* were significant for both species in accounting for variation in stomach fullness (*P. fluviatilis* full model,  $F_{1,80} = 25.96$ ,  $P < 0.001$ ; *L. gibbosus* full model,  $F_{1,68} = 13.00$ ,  $P < 0.001$ ; Table III). In the analysis of stomach fullness based on adjustment for the covariate, initial  $L_T$  was a significant contribution for *P. fluviatilis* ( $L_T$  covariate,  $F = 10.76$ ,  $P < 0.01$ ), but not *L. gibbosus* ( $L_T$  covariate,  $F = 2.91$ ,  $P > 0.05$ ).

The weakest contributions to the full model for stomach fullness were attributable to the assemblage treatment (allopatric *v.* sympatric) for *P. fluviatilis* and *L. gibbosus*, and temperature treatment (ambient *v.* heated) for *L. gibbosus*. For both *P. fluviatilis* and *L. gibbosus*, there were no significant differences in stomach fullness for individuals reared in allopatry or in sympatry at ambient or heated temperatures (Fig. 4). For *P. fluviatilis*, heated treatments generally resulted in higher stomach fullness within each set. The magnitude of this advantage differed between sets, and was significantly greater in set 2 (mean difference = 0.59%, Fisher LSD test,  $P < 0.01$ ). For *L. gibbosus*, heated treatments resulted in slightly higher stomach fullness in

TABLE II. Number of *Perca fluviatilis* and *Lepomis gibbosus* stomachs examined for diet analysis and percentage of empty stomachs from each treatment category

Treatment	$n$	Empty (%)
<i>P. fluviatilis</i>		
Heated	58	6.90
Ambient	58	3.45
Allopatric	40	2.50
Sympatric	76	6.58
<i>L. gibbosus</i>		
Heated	52	3.85
Ambient	51	1.96
Allopatric	27	3.70
Sympatric	63	3.17

TABLE III. ANCOVA for the effects of initial total length ( $L_T$ ), set, species assemblage (allopatric *v.* sympatric) and temperature treatments (ambient *v.* heated) on the stomach fullness (per cent body mass) of *Perca fluviatilis* and *Lepomis gibbosus*

Source of variation	d.f.	<i>F</i>	<i>P</i>
<i>P. fluviatilis</i>			
Intercept	1	25.96	<0.001
$L_T$	1	10.76	<0.01
Set	2	1.08	>0.05
Assemblage	1	0.34	>0.05
Temperature	1	8.61	<0.01
Assemblage $\times$ temperature	1	0.18	>0.05
Assemblage $\times$ temperature (Set)	3	0.96	>0.05
Error	80		
<i>L. gibbosus</i>			
Intercept	1	13.00	<0.001
$L_T$	1	2.91	>0.05
Set	2	3.29	<0.05
Assemblage	1	1.54	>0.05
Temperature	1	0.19	>0.05
Assemblage $\times$ temperature	1	0.05	>0.05
Assemblage $\times$ temperature (set)	3	2.40	>0.05
Error	68		

sets 1 and 3 over ambient treatment (not significant); however, stomach fullness was significantly lower in set 2 (mean difference = 0.57%, Fisher LSD test,  $P < 0.05$ ).

The diets of both *P. fluviatilis* and *L. gibbosus* consisted primarily of microcrustaceans and Chironomidae; however, there was a clear difference in the proportions of these main prey types in both species when comparing individuals maintained in the presence and absence of the other species (Fig. 5). In allopatry, the dominant prey for *P. fluviatilis* was Chironomidae (52% by volume), with microcrustaceans being the second most common prey type (21% by volume). In sympatry, the order was switched, microcrustaceans constituted a larger portion of *P. fluviatilis* diet (39% by volume), and the relative importance of Chironomidae was largely reduced (25% by volume). A very different shift was seen in *L. gibbosus* diets. In allopatry, the dominant prey in *L. gibbosus* stomachs was Chironomidae (42% by volume), followed by microcrustaceans (36% by volume). In sympatry, the relative importance of Chironomidae in *L. gibbosus* diet increased to 78% by volume and microcrustaceans were absent from the majority of *L. gibbosus* stomachs, reducing the relative importance of microcrustaceans to almost zero.

*Perca fluviatilis* *G* was not significantly correlated with the per cent by volume of microcrustaceans ( $r = 0.11$ ;  $P > 0.05$ ), nor by per cent by volume of Chironomidae ( $r = 0.05$ ;  $P > 0.05$ ) in the stomach. In contrast, *L. gibbosus* *G* was negatively correlated with the volume of microcrustaceans found in the stomach ( $r = -0.40$ ;  $P < 0.001$ ), and positively correlated with the stomach content volume of Chironomidae ( $r = 0.33$ ;  $P < 0.001$ ).

In allopatry, *P. fluviatilis* and *L. gibbosus* diet similarities (Schoener's index) were 0.89 and 0.91 in ambient and heated ponds, respectively, whereas when the two

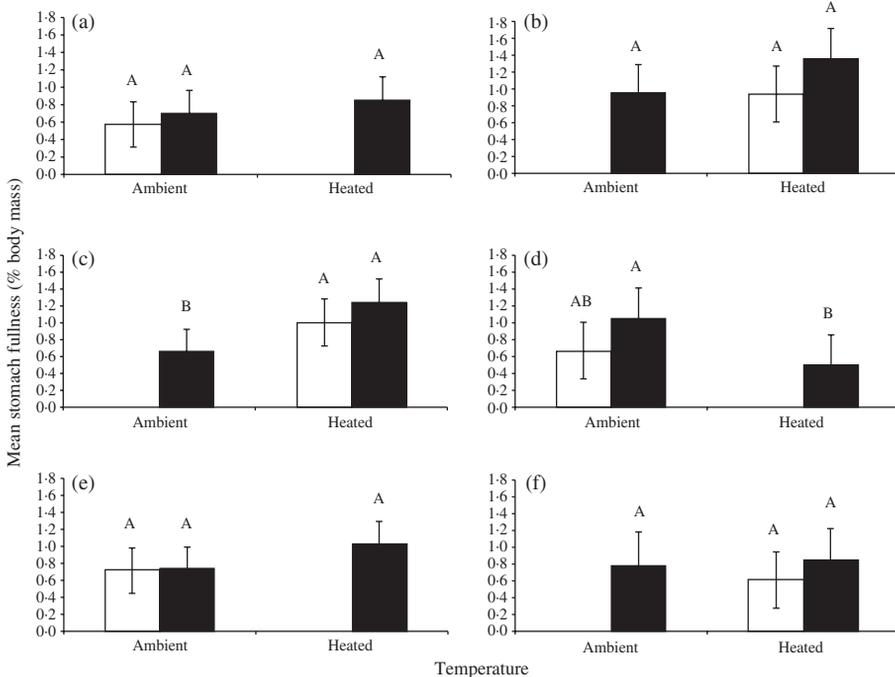


FIG. 4. Stomach fullness of (a), (c), (e) *Perca fluviatilis* and (b), (d), (f) *Lepomis gibbosus* in (□) allopatric and (■) sympatric assemblages, in ambient and heated ponds: sets (a), (b) 1, (c), (d) 2 and (e), (f) 3. Values are means  $\pm$  95% C.I. Means with different upper case letters are significantly different ( $P < 0.05$ ).

species were held in sympatry, diet similarities decreased to 0.46 and 0.27 in ambient and heated ponds, respectively. Both *P. fluviatilis* and *L. gibbosus* had high diet similarity between size classes (*P. fluviatilis*: 0.87; *L. gibbosus*: 0.78). The smaller *P. fluviatilis* ( $L_T = 81\text{--}109$  mm;  $n = 99$ ) consumed a wider variety of prey types compared with the larger *P. fluviatilis* ( $L_T = 110\text{--}141$  mm;  $n = 15$ ), and their diets included Coleoptera, Zygoptera, Trichoptera and fish (juvenile *L. gibbosus*), which were not present in the stomachs of larger *P. fluviatilis*. The larger *L. gibbosus* ( $L_T = 106\text{--}133$  mm;  $n = 54$ ) consumed a wider variety of prey types compared with the smaller *L. gibbosus* ( $L_T = 79\text{--}105$  mm;  $n = 46$ ), including Zygoptera, Anisoptera, Trichoptera and *Argyroneta* spp., The smaller *L. gibbosus* stomachs contained Plecoptera and Ephemeroptera, which were not present in the stomachs of larger *L. gibbosus*.

## DISCUSSION

The results of the growth comparison show no evidence of competitive effects between *P. fluviatilis* and non-native *L. gibbosus* in either present day (ambient) or predicted climate change (heated) environments, at least under the density conditions tested and the limited time scale of the trials. These results were unexpected, considering that in two previous competition studies on *P. fluviatilis* and *P. flavescens*,

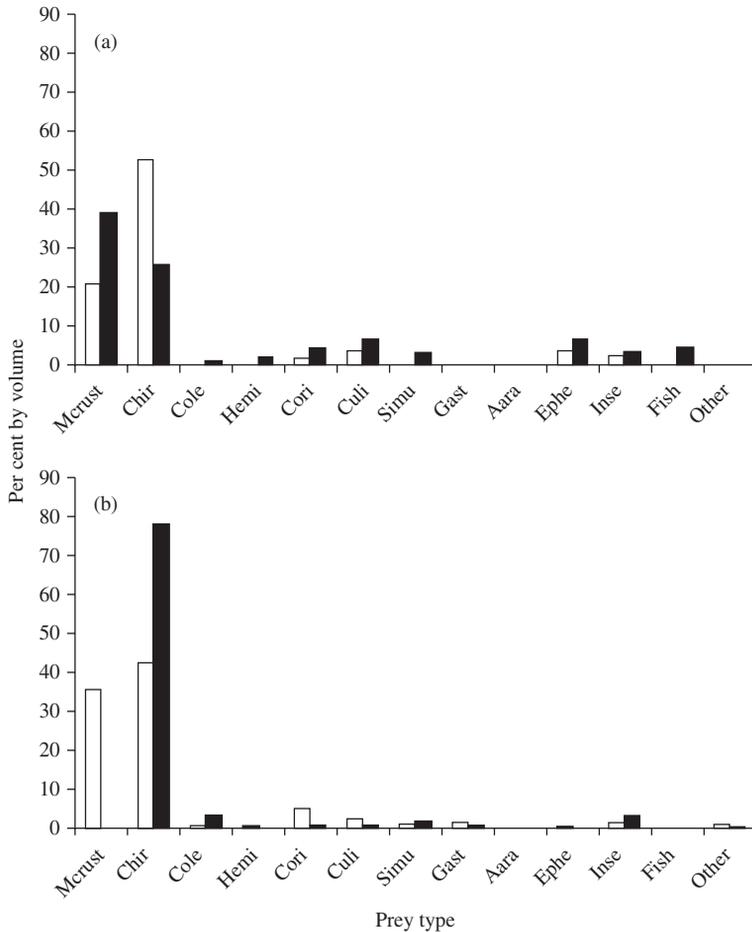


FIG. 5. Diet composition of (a) *Perca fluviatilis* and (b) *Lepomis gibbosus* in (□) allopatric and (■) sympatric assemblages. Prey types: Mcrust, microcrustaceans; Chir, Chironomidae; Cole, Coleoptera; Hemi, Hemiptera (other than Corixidae); Cori, Corixidae; Culi, Culicidae; Simu, Simuliidae; Gast, Gastropoda; Aara, Aaraneae; Ephe, Ephemeroptera; Inse, adult insect; Fish, juvenile *L. gibbosus*; Other, Anisoptera, Ceratopogonidae, Hydrachnidae, Plecoptera, Trichoptera, Tubificidae (*Tubifex* spp.), Zygoptera and plant material.

one of which involved *L. gibbosus*, the effect of the competitor on the *Perca* spp. was reduced foraging and decreased *Perca* growth, particularly under conditions of elevated temperature (Hanson & Leggett, 1985; Persson, 1986).

Temperature did have a clear effect on *P. fluviatilis* and *L. gibbosus* growth in this study, and the effect occurred in both sympatry and allopatry. Despite *P. fluviatilis* being a cool-water fish and *L. gibbosus* being a warm-water fish, both species displayed faster growth in heated ponds, and this trend was consistent over the summer. Air temperatures during the experimental period were comparable to historic mean temperatures (Meteorological Office, 2010). These results suggest that under the current climate-change models, *P. fluviatilis* in England may actually benefit from predicted increases in water temperature, as long as winter temperatures fall  $<12^{\circ}\text{C}$ ,

as higher temperatures have been shown to impede normal gametogenesis in this species (Hokanson, 1977; Sandström *et al.*, 1995; Lukšienė *et al.*, 2000). This will not necessarily be the case in warmer regions in Europe, where climate change-induced temperature increases could exceed optimal temperatures for *P. fluviatilis*.

Losses during the experiment were higher for *P. fluviatilis* than for *L. gibbosus*. This difference in number of unrecovered fishes is thought to be a reflection of higher mortality due to the fragility of *P. fluviatilis* relative to *L. gibbosus* when the species were handled and PIT-tagged, and not the result of a competitive effect. This premise is supported by the lower rate of loss of *P. fluviatilis* in sympatry than in allopatry. In fact, both species had a higher rate of loss in allopatric treatments, indicating that interspecific competition did not affect the losses of either species.

The influence of elevated temperatures on fish growth is mediated by prey resource availability. Metabolic energy demands increase as temperature rises. If sufficient food is available, then growth rates will also increase; however, if food is not available to meet these increased energy demands, then intra and interspecific competition may strengthen, and fish growth, and ultimately fitness, will be impaired (Wootton, 1998; Graham & Harrod, 2009). This was evident in the negative growth rates observed in both *P. fluviatilis* and *L. gibbosus* in the trial set of experiments.

The diet analysis revealed that competitive pressure affected prey selection, but not stomach fullness. There was no significant difference in stomach fullness of either species between allopatric and sympatric treatments; in fact, both *P. fluviatilis* and *L. gibbosus* stomachs were slightly more full in sympatric conditions. It was assumed that reduced stomach fullness is indicative of reduced food availability due to a superior competitor; however, it is possible that these two species were able to partition resources in the ponds in such a way that both were able to maintain sufficient food sources by feeding on different prey types. Although the benthic invertebrate densities decreased over the experimental season, competition did not appear to intensify with reduced prey availability (*i.e.* further reduced *G*). Thus, competition in this case did not manifest itself in the quantity of food consumed by each species, but rather in the quality of food consumed.

The diets of both *P. fluviatilis* and *L. gibbosus* in allopatric ponds, consisting predominantly of Chironomidae and to a lesser extent of microcrustaceans and other benthic invertebrates, were consistent with reports of the diet composition of similar size fishes of these species found in other water bodies (Guma'a, 1978; Zapata & Granado-Lorencio, 1993; Godinho *et al.*, 1997; Horppila *et al.*, 2000). Among-species differences in resource-use patterns in sympatry relative to allopatry are commonly interpreted as evidence for interactive segregation caused by competition among cohabiting species (Andrusak & Northcote, 1971; Wootton, 1998). In this study, *P. fluviatilis* and *L. gibbosus* reared in allopatry had very similar diets, suggesting that both species have similar prey preferences. When reared in sympatry, however, *P. fluviatilis* and *L. gibbosus* had less similar diets, indicating a clear partitioning of food resources. The diet of *P. fluviatilis* shifted from predominantly Chironomidae to primarily microcrustaceans, whereas *L. gibbosus* increased its consumption of Chironomidae relative to that of microcrustaceans.

These dietary shifts appear to be accentuated by elevated temperature, with a further 19.5% decrease in diet similarity between *L. gibbosus* and *P. fluviatilis* in the heated ponds. These results suggest temperature-dependent differences in foraging

between the two species, and that *L. gibbosus* is able to extract more resources under the temperature regimes experienced in the heated ponds (Helland *et al.*, 2011). This is likely because elevated temperatures increase the energy demand of the fish, and in sympatry it would also increase the competitive pressure, forcing a greater segregation of prey resources. These results are consistent with those of Zaret & Rand (1971), who found distinct food breadths in a stream fish community in Panama when resources were limited and thus competitive pressures were intensified, whereas fish diets were widely overlapping when resources were abundant. In the case of asymmetrical competition, which appears to be the case in this experiment, this means a greater shift to sub-optimal food choices by the weaker competitor (*i.e.* *P. fluviatilis*) to allow for both species to continue to meet increased energy demands (Declerck *et al.*, 2002; Persson & Greenberg, 1990). This distinct interactive segregation of *P. fluviatilis* and *L. gibbosus* diets supports the hypothesis that competitive pressure from the introduced *L. gibbosus*, which is intensified in heated conditions, will adversely affect the quality of food available to *P. fluviatilis*. The predicted reduction in *P. fluviatilis* growth in the presence of *L. gibbosus*, however, was not observed, and the findings that *P. fluviatilis* *G* was not affected by the relative volume of microcrustaceans in their diet, whereas *L. gibbosus* growth was inversely related to relative volume of microcrustaceans consumed, suggest the dietary shift to prey types classified as energetically inferior may not have an adverse effect on the growth of *P. fluviatilis*. It cannot be ruled out that such an effect would be manifested if the competition experiments had been run for a longer time. In any case, the difference in diet between the two species in sympatry suggests that *P. fluviatilis* will more readily shift to a microcrustacean diet when competitive pressures increase.

Although results of this study suggest that *L. gibbosus* will not adversely affect native *P. fluviatilis* growth under predicted climate change temperatures, and with the prey and competitor densities examined, concern for the effect of *L. gibbosus* under warmer conditions should not be readily dismissed. Climate change is a complex issue, and it can potentially affect fishes at all levels of biological organization, both directly and indirectly. Predictions of how climate change will affect native and non-native species are impeded by uncertainties about how multiple environmental factors will interact to influence the distribution and abundance of aquatic organisms (Lehtonen, 1996; Hellmann *et al.*, 2008; Rahel & Olden, 2008). For example, temperature can have multiple effects on reproduction; fluctuating thermal regimes can directly influence the timing and duration of spawning, and the development and survival of juvenile fishes. In an experimental study conducted in the same heated ponds used in this study, Zięba *et al.* (2010) found that *L. gibbosus* in the heated ponds began spawning earlier in the season. This seasonal shift will afford young-of-the-year *L. gibbosus* a longer first-year growing season, and accompanied by predicted milder winter temperatures (Hellmann *et al.*, 2008), will probably lead to enhanced survivorship, and thus higher *L. gibbosus* recruitment (Zięba *et al.*, 2010). Also, reproduction of *L. gibbosus* in England is currently restricted to still waters, with no spawning yet reported in lotic waters (Copp & Fox, 2007), although this is expected to change under the predicted warmer conditions of climate change (Britton *et al.*, 2010). Owing to time constraints and the small number of experimental ponds available, this study examined competition under moderate fish densities only. The effect of varying *L. gibbosus* densities on interspecific interactions were not tested; however, the anticipated switch by *L. gibbosus* in England to 'invasive' under conditions

of climate change (Britton *et al.*, 2010) is expected to result in higher densities, which are likely to exert a stronger competitive effect than examined in this study.

In summary, the growth comparison experiments and diet analysis suggest that under predicted warmer climate regimes, and at fish and prey densities examined, non-native *L. gibbosus* will have no significant influence on *P. fluviatilis* growth in England, but will probably cause a dietary shift to less optimal prey types. It is important to recognize, however, that these experiments only examined competition under predicted elevated temperatures and a short time scale, and as such, they cannot account for the complex interacting environmental factors that are likely to affect fish interactions in a climate-change future (*e.g.* shifts in food abundance and quality, increased recruitment and abundance of some species).

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