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Effects of temperature on the foraging and growth rate of juvenile common carp, *Cyprinus carpio*

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ABSTRACT

Temperature had a significant and positive effect on the foraging and growth of juvenile common carp *Cyprinus carpio* (90–105 mm) between 16 and 28 °C. Metrics measured were feeding rate (items s^{-1}), functional response (feeding rate as a function of food density), specific growth rate and incremental fork lengths. Experiments that were conducted at 16, 20, 24 and 28 °C and used two food types revealed a strong thermal influence on foraging, with the highest feeding rates achieved at 24 °C. Functional responses also revealed optimal feeding rates in relation to food density occurred at temperatures > 20 °C. Specific growth rate and incremental fork lengths were depressed at 16 and 28 °C when compared to those achieved at 20 and 24 °C. These outputs suggest an increase in foraging and growth of *C. carpio* according to a thermal gradient that were maximal between 24 and 28 °C.

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1. Introduction

Foraging performance is a major ecological parameter as animals strive to maximise their energy intake while minimising the costs associated with their searching and handling of prey (Stephens and Krebs, 1986; Galarowicz and Wahl, 2005). Thus, measuring responses of animals to food availability and environmental parameters may provide important explanatory information for observed levels of fitness, including growth rates (Mittlebach, 1981; Werner et al., 1983; Galarowicz and Wahl, 2005). Foraging performance is often quantified using the 'functional response', i.e. the feeding rate of a forager as a function of prey density (Soloman, 1949; Holling, 1959), with this important in providing insights into the dynamics of consumer–prey systems (Nilsson, 2001). Functional responses have been determined for a number of fishes, including brown trout *Salmo trutta* (Gustafsson et al., 2010), pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* (Moss and Beauchamp, 2007), lake trout *Salvelinus namaycush* (Barnhisel and Kerfoot, 2004) and walleye *Sander vitreus* (Galarowicz and Wahl, 2005). Feeding rates have been used in an invasion context to reveal superior food intake rates of invasive mosquitofish *Gambusia holbrooki* over native fishes in Iberia that assisted their invasion and resulted in declines of some native toothcarps (Caiola and de Sostoa, 2005).

The common carp, *Cyprinus carpio*, is a warm-water fish widely used in freshwater aquaculture, particularly in Central Europe (Korwin-Kossakowski, 2008), and is now present in numerous countries around the world (Lever, 1996). Where individuals have been released or escaped into the wild then invasive populations often develop and it is one of only eight fish on the IUCN list of the World's worst 100 invaders (Lowe et al., 2000). Empirical and experimental evidence suggests that water temperature is a major influence on aquaculture husbandry practices (e.g., Desai and Singh, 2009), the outcome of introductions (e.g., Britton et al., 2010a), expression of their life history traits across their range (e.g., Oygui et al., 2011), and their distribution in habitats with altered thermal regimes (e.g., Encina et al., 2008). Thus, understanding how their foraging and growth responds to temperature may provide important ecological insights useful for helping in interpreting field observations on populations in both their native and invasive range. Consequently, the aim of this paper was to experimentally determine the feeding rate, functional response and growth rate of *C. carpio* across a defined temperature range, predicting that these would increase as temperatures increase.

2. Methods

2.1. Experimental design

Juvenile common carp (starting lengths 90–105 mm, age 1, mixed parentage) were sourced from an aquaculture company in Southern England where they were being held in indoor tanks at ambient temperatures (approximately 15 °C). On arrival in the

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experimental aquaria facility, they were acclimatized to a water temperature of 16 °C for 20 day prior to the commencement of experiments. The experiments comprised of replicated bioassays in tank aquaria across a temperature range of 16, 20, 24 and 28 °C, the rationale being this range represents the typical range of summer temperatures conditions encountered by *C. carpio* over much of their range (e.g., Britton et al., 2007, 2010a). As a preliminary feeding trial revealed their foraging behaviour was inhibited when fish were placed individually in the tanks (no response to released food items), 3 fish per tank was used as they immediately responded to released food. A total of 18 tanks were used, each of 45 l and water surface area 0.14 m². They were set up in 6 vertical columns with three tanks per column, enabling use of a pump-driven, flow-through recirculation system in each column. The light: dark cycle was fixed through the period at 14: 10 h. Prior to their introduction into the tanks, the 54 experimental fish were measured (fork length, L_F, nearest mm) and weighed (W; to 0.1 g), with their mean lengths and weights being L_F: 96.5 ± 4.1 mm and W: 21.5 ± 2.5 g (± standard deviation). Significant differences in initial L_F and W between tanks and treatments were tested using ANOVAs and revealed no experimental bias resulting from using fish of significantly different sizes (Section 2.1). As fish were identifiable from their unique scale patterns, there was no need for tagging.

The experiments involved the recording of the fish feeding responses to different food densities through filming for a maximum of 5 min. The experiments were conducted over two distinct thermal periods. The first period lasted for 52 day during which the water temperature was maintained at 16 °C across all tanks; this treatment is hereafter referred to as T16. At the end of the first period, all fish were measured and weighed individually (see before), and then returned for use in the second thermal period that lasted for 50 day and used three different temperatures: 20, 24 and 28 °C (hereafter referred to as T20, T24 and T28), and replicated in 6 tanks (18 fish each). Prior to the commencement of this period, the water temperatures were elevated by 0.5 °C every 24 h and the fish acclimatized for a further 5 day. Preliminary feeding trials selected maggots and pelletized fish meal (2 mm diameter; hereafter referred to as pellets) as the released food types on the basis of their acceptability by the fish, their visibility for recording foraging behaviour and through the carp being exposed to pellets during their husbandry. In between trials, the maggots were kept in a refrigerator (approximately 4 °C) but were removed 2 h before their use and held at room temperature (16 °C). Thus, during each thermal period, the feeding rates and the functional response of the carp was quantified by presenting the fish with either maggots and pellets once daily, with the number of food items released (density) chosen randomly from 20, 30, 40, 50, 70, 100 and 150 items per tank (equivalent to 148, 222, 296, 370, 519, 740 and 1111 items m⁻², respectively, where the mean dry weight of an individual of both items was 0.011 g). The food items were released into the tanks across their entire surface area rather than a central point and all food items sank, with items taken by fish both as they fell through the water and once they had settled on the bottom of the tank. At the end of each filming, any uneaten food was removed immediately, as per Jeschke et al. (2002). The feeding response treatments were completed approximately every 72 h during each period. When the fish were not subjected to the feeding response treatments, routine feeding was maintained at 2% body weight per day, using maggots and pellets alternately.

At the end of the second period, each fish was measured and weighed. The feeding rate was the mean time taken by a fish to ingest the fifth item and expressed as the number of items taken per second. During data analyses, the use of multiple individual fish in the tanks was accounted for using linear mixed effects models (Section 2.3).

2.2. Feeding rate

Influence of temperature and food type on feeding rate was tested using ANCOVA models, while controlling the effects of food density, individual fish identity and tank position. The differences in feeding rate relative to temperature and food type were assessed by their mean differences and significance as indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons.

2.3. Functional response

The influence of food density on feeding rate was tested through determination of the functional response. Following Baker (2010), Eq. (1) was used to determine the functional response curves of food density against feeding rate for each temperature and food item as it describes the rate at which the asymptote of the functional response is reached. It was used in preference to Holling's disc equation as the latter has unrealistic and overly strict assumptions (*cf.* Holling, 1959; Mols et al., 2004; Baker et al., 2010).

$$F = \frac{aD}{(b+D)} \tag{1}$$

where F is the feeding rate, D is the prey density, a is the the asymptotic constant and b is the the half asymptotic function (Goss-Custard et al., 2006). Parameters a and b are unknown and were estimated by fitting Eq. (1) to the observed functional response data using non-linear least squared regression.

To test the effect of temperature and prey density on the functional response of *C. carpio*, linear mixed effects models were used to account for the group structure of the experiment (i.e. multiple individual fish within separate tanks). A random intercept model with tank specified as a random factor was found to be the best model (judged using Akaike's information criterion). A natural logarithmic transformation of feeding rate was required to normalise the distribution of the residuals and correct for non-linearity. The initial models included log(feeding rate) as the response variable and prey density, temperature and the interaction between these two parameters. This was completed using R 2.10.1. (R Development Core Team, 2009) and the nlme package (Pinheiro et al., 2008).

2.4. Growth rate

Growth was quantified using incremental fork length (*IFL*) and specific growth rate (*SGR*). *IFL* (mm day⁻¹) was calculated by $IFL = (FL_{end} - FL_{start})/t$, where FL_{start} and FL_{end} were the individual fork lengths at the start and at the end of each period, respectively, and t was the duration of each period (days). *SGR* (% day⁻¹) was calculated by $SGR = (W_{end} - W_{start})/t \times 100$, where W_{start} and W_{end} were the individual weights at the start and at the end of each period, respectively. The growth parameters were compared at the end of the first period (T16) using a non-parametric Kruskal–Wallis test to determine if individual fish displayed similar growth rates at 16 °C. Afterwards, growth was compared between the two periods for each temperature treatment using Mann-Whitney pairwise comparison tests. This determined whether elevated temperature resulted in significant changes in growth rates between 16 °C and the increased temperature (20, 24, and 28 °C). Finally, the growth parameters were compared during the second thermal period only to determine if individuals displayed significant growth differences between 20 and 28 °C using Kruskal–Wallis test followed by Mann-Whitney tests. Where error is provided around the mean, it represents standard error. The non-parametric tests were performed following negative results from normality test.

3. Results

3.1. Temperature and food type effects on feeding rate

The overall effects of temperature and food type on the feeding rate of *C. carpio* were significant when the effects of the other variables were controlled in the models (Fig. 1; Tables 1 and 2). Feeding rates increased significantly as water temperature increased between 16 and 24 °C, but not between 24 and 28 °C (Fig. 1; Table 1). Feeding rates of pellets were significantly higher than for maggots (Fig. 1; Table 2). In all cases, the effect of the individual fish and tank position on feeding rate was not significant (Tables 1 and 2).
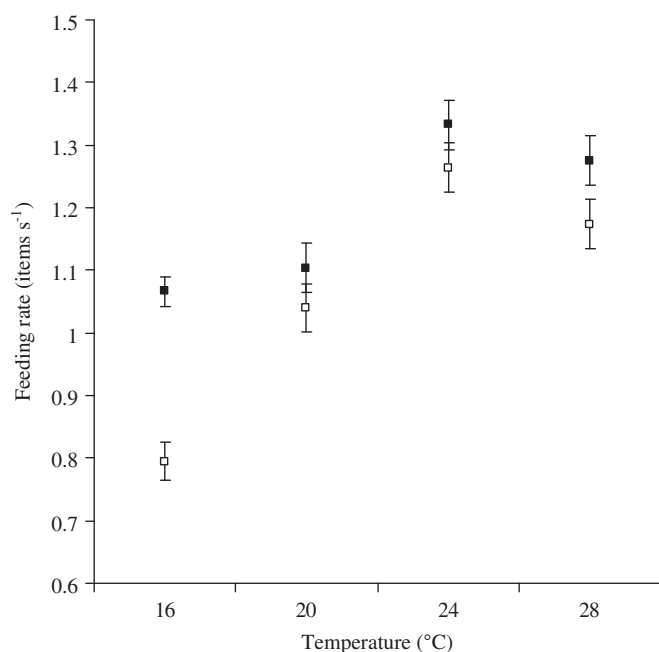
Fig. 1. Effect of water temperature on the feeding rate (time taken to consume the 5th food item) of juvenile carp where each value represents the mean feeding rate determined via ANCOVA where the effects of food density, fish identity and tank position have been controlled in the model. ■: pellets; □ maggots.

Table 1
Effects of water temperature and covariates on the feeding rate of juvenile carp (ANCOVA); Corresponding differences, indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons, between the water temperatures (16, 20, 24 and 28 °C) are displayed.

Effect		Feeding rate
Temperature		$F_{3,1236} = 45.10, P < 0.001$
Food type		$F_{1,1238} = 38.21, P < 0.001$
Food density		$F_{1,1238} = 40.79, P < 0.001$
Individual fish		$F_{1,1238} = 0.02, P > 0.05$
Tank position		$F_{1,1238} = 3.40, P > 0.05$
Difference between temperatures (mean $\pm$ S.E., items s^{-1})		
16 °C	20 °C	-0.13 ± 0.03**
	24 °C	-0.35 ± 0.03**
	28 °C	-0.28 ± 0.03**
20 °C	24 °C	-0.23 ± 0.04**
	28 °C	-0.15 ± 0.04**
24 °C	28 °C	0.07 ± 0.04

* $P < 0.05$.

** $P < 0.01$.

Table 2
Effects of food type and covariates on the feeding rate of juvenile carp (ANCOVA); corresponding differences, indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons, between the food types are displayed.

Effect		Feeding rate
Food type		$F_{1,1238} = 36.04, P < 0.001$
Temperature		$F_{1,1236} = 109.17, P < 0.001$
Food density		$F_{1,1238} = 39.86, P < 0.001$
Individual fish		$F_{1,1238} = 0.32, P > 0.05$
Tank position		$F_{1,1238} = 1.41, P > 0.05$
Difference between food types (mean $\pm$ S.E., items s^{-1})		
Maggots	Pellets	-0.15 ± 0.03**

* $P < 0.05$.

** $P < 0.01$.

3.2. Functional response

The functional responses of the juvenile *C. carpio* revealed little variation in their feeding rate over the densities of food released (Fig. 2). Feeding on pellets between the treatments T16 and T20 revealed no significant effect of prey density or temperature on feeding rate (Fig. 2(a), Table 3), but this was significant for maggots (Fig. 2(b); Table 3). Between T16 and T24, and T16 and T28, both prey density and temperature significantly affected the functional response (Fig. 2(c)–(f); Table 3). Thus, the functional response significantly increased as temperature increased, but the rate at which this increase occurred was dependent on the food source, with pellets eliciting higher feeding rates than maggots (Fig. 2).

3.3. Growth rate

The difference in L_F and W in the treatments at the commencement of the experiments was not significant (ANOVA: L_F: $F_{17,36} = 1.80, P > 0.05$; W: $F_{17,36} = 1.22, P > 0.05$). During the first thermal period at 16 °C, no significant differences in growth rates were measured (Kruskal–Wallis tests, $P > 0.05$, $n = 54$, Fig. 2; for fish in tanks T20, T24 and T28, respectively at 16 °C: *IFL*: 0.15 ± 0.01, 0.14 ± 0.01 and 0.14 ± 0.01 mm.day^{-1}; *SGR*: 0.35 ± 0.02, 0.28 ± 0.04 and 0.30 ± 0.03).

In the second thermal period, elevated water temperatures resulted in significantly higher growth rates in the three treatments (20, 24 and 28 °C) compared to the first thermal period (Mann-Whitney tests, $P < 0.05$, $n = 36$, Fig. 3), with the exception of *IFL* in T28 (Mann-Whitney test, $P > 0.05$, $n = 36$). Also, there were no significant differences were apparent in *IFL* between T20, T24 and T28 (Kruskal–Wallis tests, $P < 0.05$, $n = 54$). Significant differences in *SGR* were, however, apparent (Kruskal–Wallis tests, $P < 0.01$, $n = 54$). The *SGR* in T28 (0.48 ± 0.03) was significantly lower than T20 (0.61 ± 0.02) (Mann-Whitney comparison, $P < 0.01$, $n = 36$), but not T24 (0.56 ± 0.021) (Mann-Whitney comparison, $P > 0.05$, $n = 36$).

Thus, growth of *C. carpio* was depressed at 16 °C compared with 20, 24 and 28 °C, with some differences apparent between 20 and 28 °C, with these dependent on the growth metric being used.

4. Discussion

4.1. Thermal influences on C. carpio feeding rate, functional response and growth rate

Water temperature had a profound influence on the feeding rate, functional response and growth rate of juvenile *C. carpio*. As temperatures increased from 16 °C, the values of these parameters also increased. In general, the highest growth rates were achieved at 20 and 24 °C, and the highest feeding rate (when
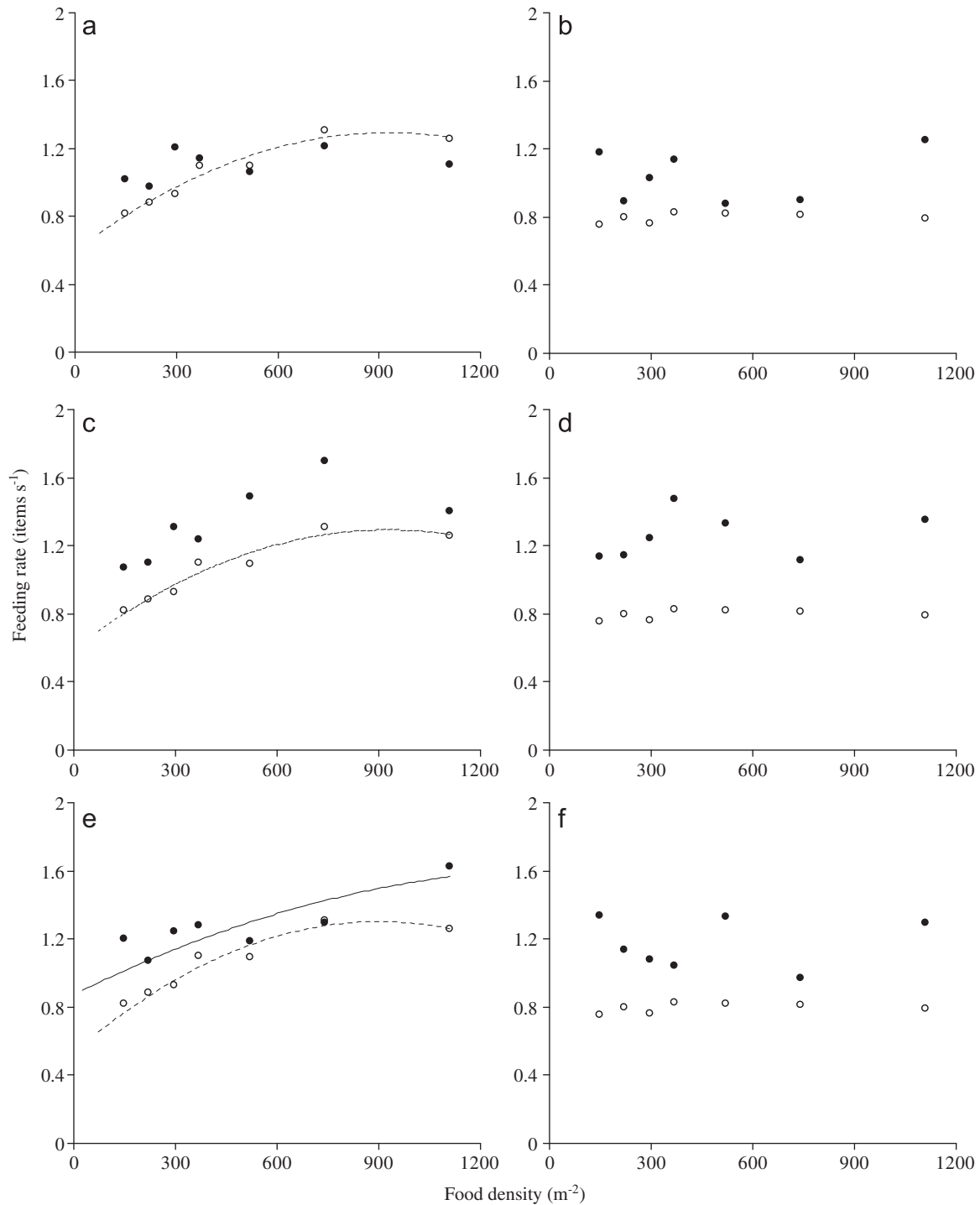
Fig. 2. Functional responses of juvenile carp in the three treatments (T20 (a–b), T24 (c–d) and T28 (e–f)) fed with pellets (a, c, e) and maggots (b, d, f). The white symbols represent the data collected during the first period (16 °C) and the black symbols represent the data collected during the second period with increased temperature in different treatments (20 °C, 24 °C and 28 °C, respectively). Where lines are shown on charts, these represent the significant relationship between food density and feeding rate ($R^2 > 0.85$, $P < 0.05$), where the dashed lines represent 16 °C and the solid lines represent the elevated temperatures (20 °C, 24 °C and 28 °C). Error bars are not displayed for brevity.

adjusted for the effects of covariates) at 24 °C. These observations were consistent across the two food types, although pellets elicited a higher feeding rate and functional response than maggots. Although reasons for this were not tested, it was noticeable that the fish responded more rapidly to the presence of pellets in the tank, whether through their audible splash on entry or through olfaction, as the pellets had a strong odour of fishmeal. Tank position and fish identity did not have a significant effect on any of the metrics.

This strong thermal influence on aspects of *C. carpio* behaviour and their life history traits is consistent with other studies on the species completed both experimentally and in the wild that show the species has a preference for warmer waters. For example, across their range, carp have the capacity to grow faster in regions of higher temperatures and longer growing seasons, with the fastest growth recorded in equatorial populations where water temperatures remain > 20 °C all year (Oyugi et al., 2011). In UK

Table 3
Outputs of the linear mixed effects models analysing differences in the functional response of juvenile carp across the different temperature treatments and food types.

Food item	Treatments	Variable	Value	Standard error	df	t	p-value
Pellet	T16–T20	Intercept	− 0.051	0.081	186	− 0.634	0.53
		Density	0.0001	0.0001	186	0.773	0.44
		Temperature	0.029	0.057	186	0.497	0.62
Pellet	T16–T24	Intercept	− 0.163	0.067	201	− 2.435	0.02
		Density	0.0004	0.0001	201	4.666	< 0.01
		Temperature	0.198	0.054	201	3.703	< 0.01
Pellet	T16–T28	Intercept	− 0.294	0.067	195	− 4.379	< 0.01
		Density	0.0004	0.0001	195	5.473	< 0.01
		Temperature	0.275	0.046	195	5.976	< 0.01
Maggot	T16–T20	Intercept	− 0.428	0.060	155	− 7.132	< 0.01
		Density	0.0002	0.000	155	2.539	0.01
		Temperature	0.288	0.052	155	5.562	< 0.01
Maggot	T16–T24	Intercept	− 0.198	0.064	166	− 3.083	< 0.01
		Density	− 0.0001	0.0001	166	− 0.785	0.43
		Temperature	0.435	0.054	166	8.040	< 0.01
Maggot	T16–T28	Intercept	− 0.430	0.089	146	− 4.811	< 0.01
		Density	0.0001	0.0001	146	1.347	0.18
		Temperature	0.445	0.060	146	7.417	< 0.01
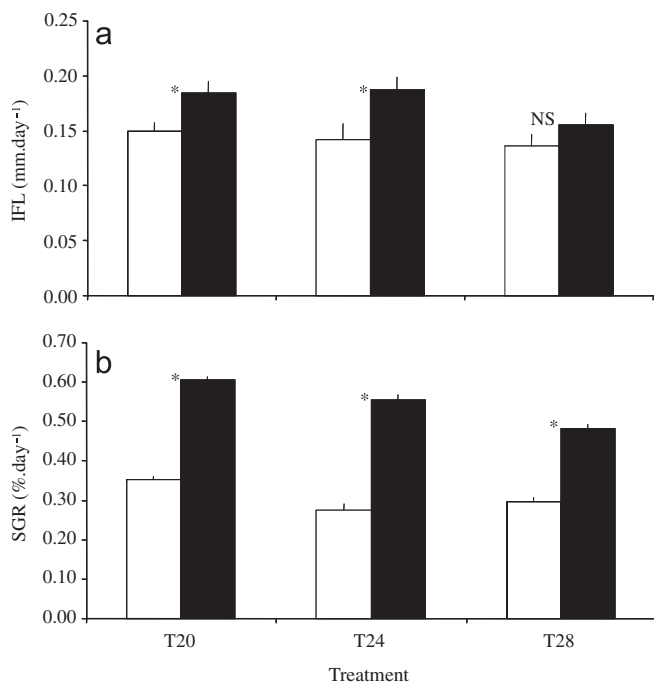
Fig. 3. Growth rates (increment fork length *IFL* (a) and specific growth rate *SGR* (b)) of juvenile carp in the three treatments (T20, T24 and T28). White columns represent data collected during the first period (16 °C) and the columns represent data collected during the second period with increased temperature in each treatments (20 °C, 24 °C and 28 °C, respectively). Error bars represent the standard errors. * $P < 0.05$. NS: non-significant.

rivers, carp have tended to live in the warmest water (about 28 °C) (Alabaster and Downing, 1966) and Økland et al. (2003) reported on a successful carp population in a warm African Reservoir where surface water temperatures reached 28 °C. Although the upper thermal of carp is not clear, Proffitt (1969) found carps are able to reside in temperatures exceeding 33 °C, although the influence of this temperature on their growth rate was not mentioned. Eaton and Scheller (1996) suggest 35 °C as their maximum tolerable temperature, and Encina et al. (2008) found that in a Spanish reservoir receiving warm water effluents, carp avoided areas of elevated temperatures in summer (41 °C).

Whilst there are few data on the thermal influences on the growth of juvenile carp, Korwin-Kossakowski (2008) revealed that the optimal temperature for their embryonic development was 26–28 °C and a short-term increase from 20 to 24 °C was sufficient to subsequently increase larval growth.

This thermal influence on aspects of *C. carpio* behaviour and their life history traits is similar to other invasive fishes, particularly in Europe (e.g. Benejam et al., 2009; Cucherousset et al., 2009; Britton et al., 2010b). Indeed, for many species in Europe, temperature is a key determinant of the outcomes of introductions, with the warmer temperatures encountered in lower latitudes enhancing growth rates and reproduction, both of which facilitate invasion success (Vondracek et al., 1988; Koya and Kamiya, 2000; Ribeiro et al., 2008). These trends between latitude, temperature and life history traits has been used to successfully explain patterns of invasion whereby populations of warm water fishes establish in some regions but not in others, such as *Lepomis gibbosus* being invasive in Southern Europe but not in Northern Europe (Cucherousset et al., 2009).

4.2. Thermal influences on the functional response

The utility of determining the influence of temperature on the functional response of a species goes beyond merely helping to explain aspects of their thermal optima. This is because they comprise fundamental components of predator–prey models where they can describe the thermal dependency of consumption rates (Englund et al., 2011). In this context, however, it is important that they provide meaningful and realistic values and this can be problematic given that experimental studies generally suffer from problems associated with scaling up to reality. This tends to result from experimental spatial constraints resulting in unnaturally intense feeding rates and laboratory conditions failing to represent more complex natural situations (Korsu et al., 2009). Nevertheless, our experiments clearly demonstrated a strong thermal effect on the feeding rate and growth of the carp and this has been at least partially corroborated by studies in the wild on carp behaviour and growth more generally (cf. Section 4.1). They are also consistent with the thermal influences on the functional responses of a number of terrestrial organisms, such as *Coccinella septempunctata* (Khan and Khan, 2010), *Adalia bipunctata* (Jalali et al., 2010) and *Habrobracon hebetor* (Bao-Zhu et al., 2009).

Whilst the functional response is temperature-dependent for many species, some studies have suggested that experimentally-derived thermal optima are often higher than the environmental temperatures the species actually experience (e.g. Deutsch et al. 2008; Huey et al. 2009). It was argued by Englund et al. (2011) that these patterns reflect experimental artefacts, as they were estimated in controlled conditions where organisms were fed *ad libitum* and temperatures were kept constant. By contrast, the same animals in the wild are exposed to conditions of food scarcity and variable temperatures, and this is important given that thermal optima can reduce as food intake decreases (Englund et al., 2011). This suggests that thermal optima estimates derived in the laboratory may be too high (Boehlert and Yoklavich, 1983). In combination, this suggests that whilst laboratory derived data are useful, some caution ought to be exercised if they are to be extrapolated to represent wild situations.

4.3. Conclusions

The experiments revealed that the foraging performance and growth rates of juvenile *C. carpio* were strongly regulated by temperature. These thermal influences were consistent with empirical studies on their wild populations that show a strong dependency on relatively warm ambient temperatures for fast growth rates and other aspects of their life history such as successful reproduction. Nevertheless, some caution may require to be exercised if these experimental data are to be used to identify the thermal optima in the wild due to the controlled conditions used in their generation.

Acknowledgments

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