

Behavioural thermoregulation in two freshwater fish species

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In the presence of a vertical thermal gradient, juvenile three-spined sticklebacks *Gasterosteus aculeatus* and minnows *Phoxinus phoxinus* positioned themselves higher in the water column compared with adult conspecifics. This result was consistent regardless of whether age cohorts were tested separately or together. Furthermore, juveniles but not adult fishes positioned themselves higher in water column in the presence of a thermal gradient compared with those in the absence of a thermal gradient. Juvenile *G. aculeatus* and adult fish of both species did opt to position themselves higher in the water column in the hours immediately following a feeding event relative to their positions in the same gradient when they had not fed.

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INTRODUCTION

Environmental temperature is of key importance to all animals but especially to ectotherms since it links directly to their rate of metabolic processes and ultimately to growth and fitness. A change in body temperature by 1°C alters the rate of many physiological processes by 6–10% (Johnston & Bennett, 1996). In a thermally heterogeneous environment, animals can sometimes employ behavioural thermoregulation, in other words, they can move to occupy areas of habitat which are thermally favourable and in doing so, regulate their temperature. Behavioural thermoregulation has been documented in many species representing many different taxa (Angilletta *et al.*, 2002; Bicego *et al.*, 2007).

Fishes represent an excellent model for the experimental study of behavioural thermoregulation, since the aquatic environment in nature often shows clear and relatively stable three-dimensional thermal heterogeneity, which can be simulated in the laboratory to provide the background against which the movements of experimental subjects may be studied. There is a wealth of evidence to indicate the use of

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behavioural thermoregulation in fishes (Beitinger & Magnuson, 1979; Reynolds & Casterlin, 1979; Matern *et al.*, 2000; Newell & Quinn, 2005; Wallman & Bennett, 2006). In some cases, this is conflated with a preference for shallow water, since in aquatic environments the temperatures at the top of the water column are often higher than those at the bottom of the water column. Occupation of shallow water, however, may also result through other mechanisms, for example, organisms may seek a refuge against predation (Cerri, 1983; Copp & Jurajda, 1993) or against strong water currents (Garner *et al.*, 1998), and it is clearly important to distinguish between these mechanisms and behavioural thermoregulation.

If a fish chooses to occupy a position at the top of the water column, it may have to trade the benefit of increased metabolic efficiency against reduced food availability and increased predation threat, since it increases an individual's exposure to surface-feeding avian predators, and possibly also to some piscine predators. The cost-to-benefit ratio may be different for smaller, juvenile fishes than for larger adults in warmer, surface waters, because while small fishes have potentially more to gain from increasing their growth rate (especially if the adults are not producing gametes) they also have a higher mass-specific metabolic rate and need to feed more often (Krause *et al.*, 2000) and are vulnerable to a larger variety of predators. Hence, a number of factors may govern the decision of fishes to occupy positions at the top of the water column, including the existence and the size of a thermal gradient, the stage in the fish's life cycle and its satiety.

In this study, the hypothesis that fishes would elect to occupy a different position in the water column in the presence of a thermal gradient compared with a control condition in which the water column was of a uniform temperature was tested. It was predicted that juvenile fishes would occupy surface waters more often than adults in order to maximize growth rate. It was further predicted that recently fed fishes would use the warmer water at the surface to a greater extent than those that were food deprived in order to maximize metabolic efficiency. Two distantly related species were tested in order to assess the generality of the predictions.

MATERIALS AND METHODS

STUDY ANIMALS

Three-spined sticklebacks *Gasterosteus aculeatus* L. are widely distributed in fresh and marine waters across the northern hemisphere and from latitudes north of the Arctic Circle to North Africa (Bell & Foster, 1994). Minnows *Phoxinus phoxinus* (L.) occur primarily in fresh water from Spain to Siberia, and from 37 to 73° N (Froese & Pauly, 2009). Both species occupy a wide range of thermal conditions across their ranges. The fishes used in this study were collected in late September to October 2003 from the River Welham, Leicestershire, U.K. (52° 30' 34.5" N; 0° 52' 18.2" W). Before the beginning of experiments, the fishes were held for between 3 and 4 weeks in 30 l aquaria at 14° C. They were fed *ad libitum* daily with defrosted frozen bloodworm *Chironomus* sp. At this time of year, two distinct size classes may be observed both for *G. aculeatus* and for *P. phoxinus*. Young of the year (YOY, 0+ years) *G. aculeatus* typically measure 15–25 mm standard length (L_S), whereas adults (1+ years) measure >35 mm L_S , although in this study for the 1+ year age cohort, fish between 38 and 45 mm L_S were selected. YOY *P. phoxinus* measure 20–27 mm L_S , whereas 1+ year fish measure >40 mm L_S , and fish between 50 and 60 mm L_S were selected for the 1+ year cohort.

EXPERIMENTAL DESIGN AND PROTOCOL

Six aquaria were sited in a controlled temperature room at the University of Leicester. The aquaria were constructed from marine plywood coated with a non-toxic resin. Each aquarium had a front glass panel for viewing aquarium occupants. The aquaria, measuring 40 cm × 40 cm × 100 cm (length × width × height), were filled to a depth of 90 cm. All of the six aquaria were then subject to one of two different water temperature treatments, either (1) a constant water temperature of 14° C throughout each aquarium or (2) a vertical temperature gradient ranging from 11.0° C range $\pm 0.5^\circ$ C at a depth of 85 cm to 17.0° C range $\pm 0.5^\circ$ C at a depth of 5 cm. Measurements taken at 10 cm intervals indicated that the gradient was even both horizontally and vertically throughout the water column in each aquarium, and that the temperature of the midpoint of the column was 14° C.

The constant water temperature treatment was achieved by setting the room temperature to 14° C. The water temperature gradient conditions were established by setting the room temperature to 10° C and adding a thermostatically controlled 250 W aquarium heater set to 20° C to the aquarium at a depth of 65 cm.

The water conditions were allowed to stabilize for 72 h before adding fishes. To control for the presence of an aquarium heater in the water temperature gradient treatment, aquarium heaters were added to the constant water temperature treatment although these were switched off in this case. Once the 72 h had elapsed, a group of six fishes was added to each aquarium. Fishes were tested in groups since both *P. phoxinus* and *G. aculeatus* are social species.

The fishes were left to acclimatize for 3 weeks during which time they were fed *ad libitum* daily with defrosted frozen bloodworms. The bloodworms, which were in 100 ml of water, were poured into the tank in order to distribute them as evenly as possible throughout the aquarium. In addition, the food was presented to the fishes at different times of day throughout to prevent food anticipatory behaviour whereby animals gather at a feeding station before a fixed feeding time (Reeb, 1996). Levels of ammonia were monitored and remained low throughout the experimental period. Finally, to minimize disturbance, the aquaria were concealed in housings made of black plastic that covered the top and the front viewing panel (set back at a distance of 0.9 m from the glass) with the exception of a narrow vertical strip to act as a viewing aperture. Neither filtration nor aeration was used since this would have disturbed the thermal gradient.

Following the 3 weeks of acclimation, observations were made of the fishes' positions every 2 h for a total of 24 h. The observations were made by taking a single photograph using a Nikon Coolpix digital camera (www.nikon.com); flash was not used in order to avoid startling the experimental subjects, although a 50 W bulb was used to light the room during the night period in order to facilitate photography. After each batch of experimental replicates, the fishes were removed, the water was changed and the process was repeated with new fishes.

TREATMENTS

In the first experiment, four treatments were run in a 2 × 2 design with fish age (0+ or 1+ years) and water temperature (presence or absence of thermal gradient) as the variables. Twelve replicates were completed for each treatment.

In the second experiment, the age cohorts were combined and the two water temperature treatments were run again with new fishes. Eight replicates were completed for each treatment. In the first two experiments, fishes were not fed within 12 h of the start of the observations.

In the third experiment, four treatments were run using the same 2 × 2 design described previously. This case differed in that the experimental fishes were fed 1 h before observations and five 2 h observations of fish position in the water column were taken. Twelve replicates were completed for each treatment.

A group of six fishes was used for each experimental replicate. In experiments 1 and 3, each group was comprised of fishes of the same age group. In experiment 2, three 0+ year fish and three 1+ year fish were used.

The full experimental protocol was run twice, once with *G. aculeatus* and once with *P. phoxinus*. Each individual fish was used only once.

DATA ANALYSIS

The response variable, fish height in the water column, was obtained from the photographs. A single fish was chosen from the group (or in the case of the mixed age groups, two fish, one representing each cohort) using a randomization procedure derived from www.random.org. To analyse the data, a mixed between and within-subjects repeated measures ANOVA was used. Mauchly's test of sphericity was always significant for the time variable, indicating that the assumption of sphericity had been violated. Exact multivariate test results (Pillai's trace) are therefore presented instead of univariate results. *P* values for single between-subjects comparisons were compared with Bonferroni-adjusted criteria for significance that were calculated separately for each species. All analyses were performed in SPSS 16.0.2 (www.spss.com).

RESULTS

In the first experiment, there were significant effects of time, age and thermal gradient on both species (Table I and Fig. 1). Where there was no thermal gradient, all fishes tended to occupy a similar position towards the bottom of the water column. The presence of a thermal gradient affected only juvenile fishes; they occupied a higher position in the tank when a gradient was applied, in contrast with the older fishes that did not alter their position in the water column (Table II). The thermal \times age interaction confirms that the presence of a thermal gradient affected the difference in water column height between fishes of different ages. The age \times time interaction indicates that fishes of different ages showed different temporal variation in water column height, this was only seen in *G. aculeatus*. The thermal \times time interaction indicates that the presence of a thermal gradient affected the trend in distance from the water surface over time; in *P. phoxinus*, the application of a thermal gradient reduced the amount of variation in distance from the water surface over time.

There was no difference between the behaviour of either *P. phoxinus* or *G. aculeatus* (general linear model, GLM, both d.f. = 1,63, *P* > 0.05) in single cohort v. mixed cohort treatments.

In the third experiment, there were significant effects in both species for all four main factors: time, age, thermal gradient and food (Table III and Fig. 2). In the presence of a thermal gradient, adult *P. phoxinus* and juvenile and adult *G. aculeatus* occupied positions higher in the water column immediately following feeding than

TABLE I. Main effects from combined model (two-way mixed between and within-subjects repeated measures ANOVA). Fishes were not fed immediately before experiment

Source of variation	<i>Phoxinus phoxinus</i>			<i>Gasterosteus aculeatus</i>		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Time	3.36	11	<0.01	13.83	11	<0.01
Age	151.76	1	<0.01	37.89	1	<0.01
Thermal	142.16	1	<0.01	44.60	1	<0.01
Age \times thermal	116.90	1	<0.01	46.80	1	<0.01
Time \times age	0.64	11	>0.05	3.13	11	<0.01
Time \times thermal	2.86	11	<0.01	1.47	11	>0.05
Time \times age \times thermal	0.47	11	>0.05	1.37	11	>0.05

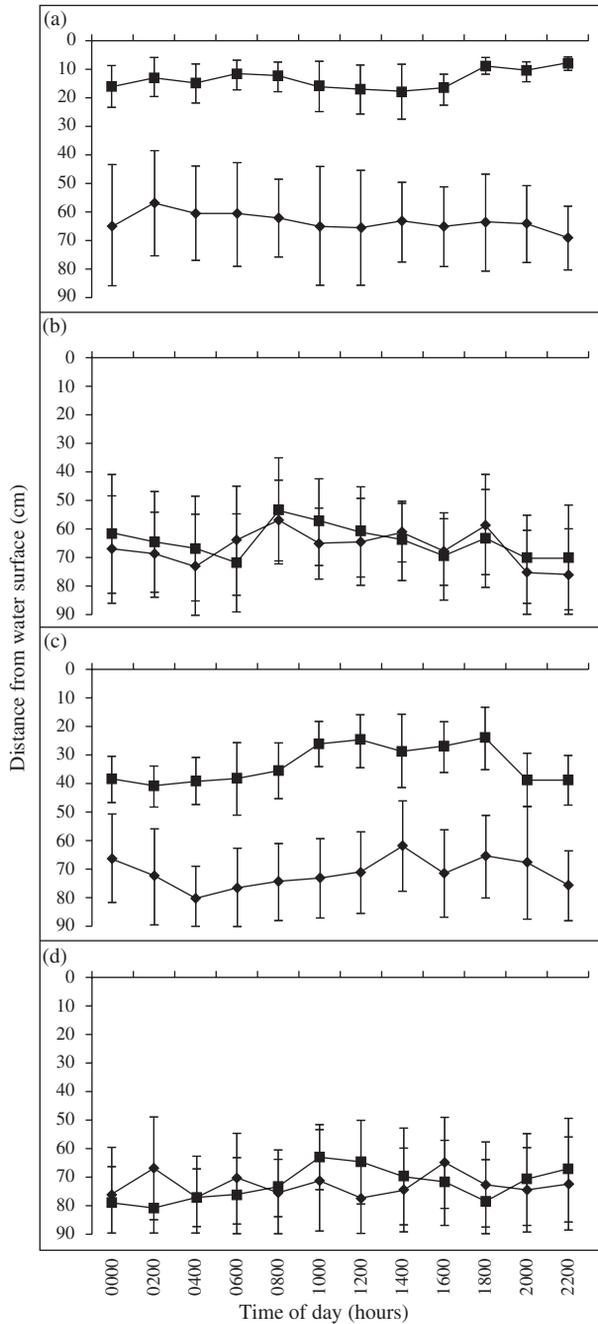


FIG. 1. Mean \pm s.d. distance from the surface as a function of time is shown for juvenile (0+ years; ■) and adult (1+ years; ◆) fishes. *Phoxinus phoxinus* in (a) a thermal gradient and (b) an isothermic environment, and *Gasterosteus aculeatus* in (c) a thermal gradient and (d) an isothermic environment ($n = 12$ for each).

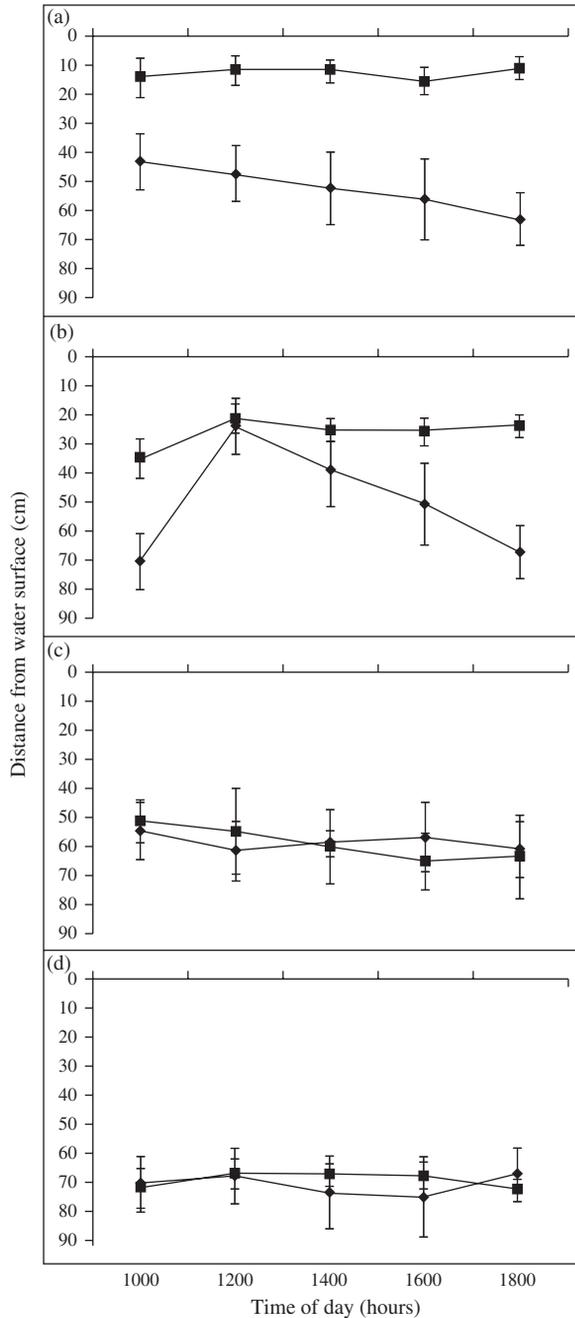


FIG. 2. Mean \pm s.d. distance from the surface as a function of time following a feeding event at 0900 hours is shown for juvenile (0+ years; ■) and adult (1+ years; ◆) fishes. (a) *Phoxinus phoxinus* in a thermal gradient and (b) *Gasterosteus aculeatus* in a thermal gradient and (c) *P. phoxinus* in an isothermic environment and (d) *G. aculeatus* in an isothermic environment ($n = 12$ for each).

TABLE II. Mixed between and within-subjects repeated measures ANOVA, showing (a) comparisons between juvenile and adult *Phoxinus phoxinus* and *Gasterosteus aculeatus* and (b) comparisons between the presence and absence of a thermal gradient. Fishes were not fed immediately before experiment

Species	Age (years)	No gradient mean \pm S.E. distance (cm) from surface	Gradient mean \pm S.E. distance (cm) from surface	d.f.	F	P*
<i>P. phoxinus</i>	0+	64.4 \pm 1.6	13.7 \pm 1.0	1	348.97	<0.001
<i>P. phoxinus</i>	1+	66.5 \pm 1.8	63.5 \pm 0.9	1	0.75	>0.05
<i>G. aculeatus</i>	0+	72.8 \pm 1.7	33.4 \pm 1.9	1	114.71	<0.001
<i>G. aculeatus</i>	1+	72.8 \pm 1.2	71.4 \pm 1.5	1	0.11	>0.05

Species	Thermal gradient	Age 0+ years mean \pm S.E. distance (cm) from surface	Age 1+ years mean \pm S.E. distance (cm) from surface	d.f.	F	P*
<i>P. phoxinus</i>	0	64.4 \pm 1.6	66.5 \pm 1.8	1	0.31	>0.05
<i>P. phoxinus</i>	1	13.7 \pm 1.0	63.5 \pm 0.9	1	517.04	<0.001
<i>G. aculeatus</i>	0	72.8 \pm 1.2	72.8 \pm 1.2	1	0.00	>0.05
<i>G. aculeatus</i>	1	33.4 \pm 1.9	71.4 \pm 1.5	1	131.28	<0.001

*Bonferroni-adjusted criterion for significance $P = 0.013$.

TABLE III. Main effects from combined model (two-way mixed between and within-subjects repeated measures ANOVA). *Phoxinus phoxinus* and *Gasterosteus aculeatus* were fed immediately before experiment

Source of variation	<i>P. phoxinus</i>			<i>G. aculeatus</i>		
	d.f.	F	P	d.f.	F	P
Time	4	3.99	<0.01	4	10.49	<0.001
Age	1	226.49	<0.001	1	77.86	<0.001
Thermal	1	282.94	<0.001	1	207.06	<0.001
Food	1	15.97	<0.001	1	12.28	0.001
Age \times thermal	1	227.34	<0.001	1	64.21	<0.001
Age \times food	1	3.19	>0.05	1	2.27	>0.05
Thermal \times food	1	1.24	>0.05	1	10.31	<0.01
Time \times age	4	1.59	>0.05	4	1.16	>0.05
Time \times thermal	4	0.43	>0.05	4	3.44	<0.05
Time \times food	4	3.32	<0.05	4	6.78	<0.001
Age \times thermal \times food	1	2.32	>0.05	1	1.71	>0.05
Time \times age \times thermal	4	3.22	<0.05	4	10.55	<0.001
Time \times age \times food	4	0.93	>0.05	4	10.23	<0.001
Time \times thermal \times food	4	0.68	>0.05	4	7.41	<0.001

they did in trials where they had not recently fed (Table IV and Fig. 2). Echoing the results of the first experiment, juvenile fishes of both species occupied higher positions in the water column than did adults, regardless of the feeding treatment

TABLE IV. Mixed between and within-subjects repeated measures ANOVA, showing (a) comparisons between juvenile and adult *Phoxinus phoxinus* and *Gasterosteus aculeatus* and (b) comparisons between the presence and absence of a thermal gradient. Fishes were fed immediately before experiment

Species	Age (years)	Thermal gradient	Food mean \pm s.e. distance (cm) from surface	No food mean \pm s.e. distance (cm) from surface	d.f.	F	P*
<i>P. phoxinus</i>	0+	0	59.12 \pm 1.75	62.97 \pm 1.27	1	0.92	>0.05
<i>P. phoxinus</i>	0+	1	12.75 \pm 0.56	15.4 \pm 1.07	1	3.97	>0.05
<i>P. phoxinus</i>	1+	0	58.68 \pm 0.85	63.32 \pm 1.09	1	2.82	>0.05
<i>P. phoxinus</i>	1+	1	52.23 \pm 2.25	64.63 \pm 0.28	1	16.73	<0.001
<i>G. aculeatus</i>	0+	0	69.48 \pm 0.83	69.61 \pm 1.82	1	0.02	>0.05
<i>G. aculeatus</i>	0+	1	26.27 \pm 1.54	31.18 \pm 0.51	1	12.19	<0.01
<i>G. aculeatus</i>	1+	0	70.95 \pm 1.00	72.07 \pm 1.39	1	0.05	>0.05
<i>G. aculeatus</i>	1+	1	50.45 \pm 5.75	68.62 \pm 1.40	1	18.89	<0.001

Species	Thermal	Food	0+ years mean \pm s.e. distance (cm) from surface	1+ years mean \pm s.e. distance (cm) from surface	d.f.	F	P*
<i>P. phoxinus</i>	0	0	62.97 \pm 1.27	63.32 \pm 1.09	1	0.01	>0.05
<i>P. phoxinus</i>	0	1	59.12 \pm 1.75	58.68 \pm 0.85	1	0.25	>0.05
<i>P. phoxinus</i>	1	0	15.4 \pm 1.07	64.63 \pm 0.28	1	443.81	<0.001
<i>P. phoxinus</i>	1	1	12.75 \pm 0.56	52.23 \pm 2.25	1	283.35	<0.001
<i>G. aculeatus</i>	0	0	69.61 \pm 1.82	72.07 \pm 1.39	1	0.13	>0.05
<i>G. aculeatus</i>	0	1	69.48 \pm 0.83	70.95 \pm 1.00	1	0.18	>0.05
<i>G. aculeatus</i>	1	0	31.18 \pm 0.51	68.62 \pm 1.40	1	98.54	<0.001
<i>G. aculeatus</i>	1	1	26.27 \pm 1.54	50.45 \pm 5.75	1	92.20	<0.001

*Bonferroni-adjusted criterion for significance $P = 0.006$.

(Table IV and Fig. 2). There was a significant three-way interaction between time, age and thermal gradient in both species (Table III). In the absence of a thermal gradient, both adult and juvenile fishes showed considerable temporal variation in mean distance from the water surface; at the start of the experiment juveniles were closer to the water surface than adults, but over the course of the observation period this trend reversed, so that by the end the adults were closest to the surface. In the presence of a thermal gradient, not only was temporal variation in position reduced in all fishes, but juveniles of both species consistently occupied higher positions in the water column than the adults throughout the observation period. In *P. phoxinus* the feeding treatment had no effect on the relationship between age or thermal gradient and temporal variation in position (Table III). In contrast, adult *G. aculeatus* occupied lower positions than juveniles from the outset in the absence of food, but immediately after feeding they started at the same height as the juveniles, before gradually moving to lower positions. In the absence of a thermal gradient, the *G. aculeatus* consistently occupied low positions in the water column irrespective of feeding treatment. When a thermal gradient was present they occupied higher positions in the water column under both feeding conditions, but the effect was pronounced immediately after

feeding; fed fish started the observation period close to the water surface (22.5 cm) and then gradually moved deeper as the trial progressed, eventually reaching *c.* 50 cm (the depth at which those that had not received food remained throughout the trial).

DISCUSSION

In the presence of a thermal gradient, juvenile fishes positioned themselves higher in the water column than adult conspecifics. This result was consistent regardless of whether age cohorts were tested separately or together. Furthermore, juveniles but not adult fishes positioned themselves higher in water column in the presence of a thermal gradient than in the absence of a thermal gradient. Juvenile *G. aculeatus* and adult fish of both species did opt to position themselves higher in the water column in the hours immediately following a feeding event relative to their positions in the same gradient when they had not fed.

Juvenile fishes demonstrated a preference for warmer waters, possibly to facilitate growth (Elliott, 1975; Wootton, 1990; Hofmann & Fischer, 2003) since mortality due to predation and the stresses imposed by undergoing a first winter season is large for the young of many species. Nonetheless, in many cases, fishes are thought to select temperatures that maximize their physiological performance, or their growth efficiency rather than their absolute growth rate (Wildhaber & Crowder, 1990; Larsson, 2005). The potential trade-off between increased predation risk in surface waters and elevated metabolism may be mediated by faster reaction speeds of warm muscles (Beamish, 1978; Kelsch, 1996); however, the idea that a position high in the water column may be associated with increased costs is at least suggested by the deeper positions occupied by juveniles in the absence of a thermal gradient. The findings suggest that they are not driven there by competition from adults. Evidence suggests that distribution of different age cohorts within wild fish populations is closely related to temperature, with smaller fishes generally preferring warmer temperatures (Wildhaber & Crowder, 1990; Garner *et al.*, 1998; Wildhaber, 2001; Hattori & Warburton, 2003; Gauthier & Rose, 2005). This same ontogenetic shift in thermal preferences wherein juveniles select relatively higher temperatures than adults is widespread across taxa, including insects (Kuhrt *et al.*, 2005), crustaceans (Ouellet & Allard, 2006) and amphibians (Bancroft *et al.*, 2008). In some reptiles, however, the pattern is reversed, possibly as smaller individuals seek to limit the risks imposed by exposure during basking (Webb & Whiting, 2005; Herczeg *et al.*, 2007).

A migration to warmer waters in the hours following feeding was observed for adults of both species, as well as for juvenile *G. aculeatus*, and there was a non-significant trend for this in juvenile *P. phoxinus*. The move was less marked in juveniles following the feeding event possibly because the scope for increasing their height in the water column was much reduced relative to adults. In addition, adults gradually moved back to deeper water as time since feeding increased, which may reflect a general preference of adult fishes for comparatively lower temperatures (McCauley & Casselman, 1980; Jobling, 1981), and as mentioned previously, the optimal temperature for metabolic efficiency may be lower than that for growth (Jobling, 1997). The interaction of habitat preference and nutritional state has been recorded in many ectothermic animals. For example, black rat snakes *Elaphe obsoleta obsoleta* (Say) seek out warmer areas of habitat in both controlled laboratory

experiments as well as in the field [Blouin-Demers & Weatherhead (2001); however, Wall & Shine (2008) provide alternative view]. Seeking out colder area of habitat during periods of food deprivation offers ectotherms a means of conserving energy, a strategy used by the lizard *Anolis carolinensis* (Brown & Griffin, 2005). Similarly, chum salmon *Oncorhynchus keta* (Walbaum) are thought to minimize energetic expenditure during migration by preferentially travelling in cooler waters (Tanaka *et al.*, 2000).

Many species of fishes across a wide variety of different habitats demonstrate daily as well as seasonal migration patterns that are assumed to be at least partly driven by behavioural thermoregulation (McCauley & Huggins, 1979; Matern *et al.*, 2000; Newell & Quinn, 2005). Variation in the response of fishes of different ages to thermal heterogeneity may also play a role in shaping population level patterns. For example, the pattern of size assorted fish shoals in the wild (Ward & Krause, 2001) may be driven at least partly by thermal habitat preferences since this would cause fishes of different sizes to segregate in their environment. In addition to thermal conditions, other factors may influence the habitat choice of fishes, including illumination and pressure (Pavlov *et al.*, 2000).

Interesting further work would include an examination of the preference of juvenile fishes for warmer waters with their observed preferences for shallows to understand whether these preferences are driven by different behavioural imperatives. For example, surface waters are avoided because they are associated with greater risk, and this behaviour may be mediated by group size since individuals in larger groups benefit from risk dilution (Krause & Ruxton, 2002). An integrated understanding of this would be extremely useful in attempts to effectively manage aquatic habitats.

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