The trade-off between growth rate and locomotor performance varies with perceived time until breeding

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SUMMARY
Environmental circumstances can cause changes in early growth patterns that subsequently affect the adult phenotype. Here we investigated how different growth trajectories affected subsequent locomotor performance, and how such effects were influenced by the perceived time until the key life-history event of reproduction. Using juvenile three-spined sticklebacks Gasterosteus aculeatus, we show that a brief period of manipulated temperature in early life (independent of food supply) caused effects on skeletal growth trajectory not only during the manipulation itself, but also during a subsequent compensatory phase. The outcome of these changes was that fish in all treatment groups reached the same average size by sexual maturity, despite having different growth patterns. However, their growth trajectory had impacts on both pre-breeding swimming endurance and its decline over the course of the breeding season, such that swimming ability was negatively correlated with skeletal growth rate during the compensation period. We also show for the first time that ‘negative compensation’ (i.e. a decelerating growth trajectory) led to an improved swimming performance compared with steadily growing controls. Replicate experiments and photoperiod manipulations, moreover, revealed that the effects of growth rate on subsequent swimming performance were greater when the perceived time until the breeding season was shorter. These results show that the costs of accelerated or decelerated growth can last well beyond the time over which growth rates differ, and are affected by the time available until an approaching life history event such as reproduction, possibly because of the time available to repair the damage.

Key words: stickleback, growth, fish, swim, temperature, photoperiod.

INTRODUCTION
Environmental circumstances in early life can cause changes in the tempo and pattern of growth and development (Weatherley and Gill, 1987). Although an episode of poor conditions can cause a slowing of growth, if adequate supplies are subsequently restored, normal adult size can still be reached by growth acceleration (Dobson and Holmes, 1984; Miglavs and Jobling, 1989; Quinton and Blake, 1990). A large body size may often be beneficial [e.g. resulting in reduced predation rate or increased fecundity (Arendt, 1997), or increased prey choice (Ludsín and DeVries, 1997)]. However, recent studies in several taxa have shown that the accelerated growth rate required to achieve a large size after a period of poor growth can carry costs: for instance, faster growth in early life is linked to earlier mortality in adult life (Rollo, 2002; Metcalfe and Monaghan, 2003; Ricklefs, 2006). Therefore animals may face continual trade-offs between the benefits and costs of growth compensation.

Although many studies of the effect of growth rate on later performance have focussed on the level or quality of nutrition (Miglavs and Jobling, 1989; Álvarez and Metcalfe, 2005; Inness and Metcalfe, 2008), this is not the only cause of variation in growth rate. For ectotherms, environmental temperature has major effects on growth and metabolism, independent of food supply (Guderley, 1994). Thermal conditions can limit their rate of growth and development, because colder temperatures limit the rate at which they can capture and digest food, and temperatures close to upper tolerance limits result in poorer growth due to high metabolic costs (Brett, 1979; Gadomski and Caddell, 1991). Temperature acclimation leads many species to adjust tissue metabolic capacities (Rome et al., 1984; Sisson and Sidell, 1987), but changes in environmental temperature have effects on energy budgets (Guderley, 2004), lipid levels and activity patterns (i.e. changes in foraging rate) (Hurst et al., 2005). As a result, a period of atypically cold temperatures can cause animals to drop below their normal growth trajectory, even if food has been freely available throughout (Niciez and Metcalfe, 1997), because they cannot swim as fast to capture moving food items and intervals between meals are longer because of the reduced speed of digestion (Wotton, 1998).

Growth opportunity may also be influenced by seasonal factors (Boeuf and Le Bail, 1999). Photoperiod is one of the most important abiotic factors affecting growth and survival (Battaglene, 1995; Boeuf and Le Bail, 1999). Many diurnal animals are visual predators and therefore require light for feeding, so that the duration of daylight may constrain food intake by limiting the period of daily foraging (Blaxter, 1980). The photoperiod also indicates the time of year, and hence potentially the time available until the end of the growing season or some other event when body size or reserves are strongly linked to fitness (e.g. hibernation, reproduction). Animals may therefore be expected to increase their growth rate if there is a reduction in the perceived time available before such key life history events (Nylin and Gotthard, 1998; Metcalfe and Monaghan, 2001). However, responses of animals to photoperiod cues of growth opportunity are poorly understood: an experimental shift in the photoperiod (simulating a shorter time until the end of the growing season) has been found to cause accelerated growth in some insect
larvae (Nylin and Gotthard, 1998), whereas other studies (e.g. De Block et al., 2008) found that the rate of compensatory growth in response to an earlier period of either food shortage or cool temperatures was not stronger under a time constraint.

Changes in growth rate may also result in physiological changes in the animal. For instance, the accelerated growth of fish due to changing temperatures influences muscle cellularity and development (Galloway et al., 1999; Johnston, 2003). In many species, adjustment to low temperatures also increases tissue aerobic capacities (Guderley, 1990; Johnston, 1993; Guderley and St Pierre, 1996). Such effects on metabolism and musculature are likely to lead to changes in locomotor performance, and indeed rapid growth has been associated with reduced sustained and burst swimming performance in fish (Kolok and Oris, 1995; Billerbeck et al., 2001; Arnott et al., 2006). However, the studies to date have tended to make a single measurement of locomotor performance (usually during a period of rapid growth), and so the longer term consequences of changes in growth trajectory are little known.

The aim of this study was to investigate how different growth trajectories affected locomotor performance (in both the short and long term), and how any such effects were dependent on the time available until a point when body size has known fitness consequences (i.e. the breeding season). For this study, we chose three-spined sticklebacks (*Gasterosteus aculeatus* L.) because they are known to exhibit compensatory growth (Wootton, 1998; Álvarez and Metcalfe, 2005; Inness and Metcalfe, 2008), possibly as a result of their reproductive success being size dependent (Kraak and Bakker, 1998; Kraak et al., 1999), and their swimming performance has previously been found to be compromised by compensatory growth (Álvarez and Metcalfe, 2005; Álvarez and Metcalfe, 2007). However, in these earlier studies the compensatory growth was induced by changing food levels, and so the effect might have been different to the earlier period of undernutrition rather than the compensation *per se*. Therefore, in the present study food was always available *ad libitum* (so fish were always in good nutritional condition) and the different growth patterns (i.e. acceleration, deceleration, and steady) were induced by manipulations of environmental temperature. We were thus able to test how effects of temperature on early growth trajectory influenced subsequent changes in locomotor performance, independent of any effect of nutrition. We examined the effect of seasonal influences on the trade off between growth performance, independent of any effect of nutrition. We examined the effect of seasonal influences on the trade off between growth performance and later life history consequences (i.e. the breeding season). For this study, we chose three-spined sticklebacks because they are known to exhibit compensatory growth (Álvarez and Metcalfe, 2005; Inness and Metcalfe, 2008), possibly as a result of their reproductive success being size dependent (Kraak and Bakker, 1998; Kraak et al., 1999), and their swimming performance has previously been found to be compromised by compensatory growth (Álvarez and Metcalfe, 2005; Álvarez and Metcalfe, 2007). However, in these earlier studies the compensatory growth was induced by changing food levels, and so the effect might have been different to the earlier period of undernutrition rather than the compensation *per se*. Therefore, in the present study food was always available *ad libitum* (so fish were always in good nutritional condition) and the different growth patterns (i.e. acceleration, deceleration, and steady) were induced by manipulations of environmental temperature. We were thus able to test how effects of temperature on early growth trajectory influenced subsequent changes in locomotor performance, independent of any effect of nutrition. We examined the effect of seasonal influences on the trade off between growth performance and later life history consequences (i.e. the breeding season).

### MATERIALS AND METHODS

#### Fish and rearing conditions

The breeding season of sticklebacks in the source population begins in May. Therefore, in order to see whether the compensatory growth response differs (i.e. is more marked, with stronger effects on swimming performance) when the time available for growth prior to the onset of the breeding season is short, the experiment was run twice, with the main manipulation of growth rates through temperature occurring either a long (the Winter experiment) or short (the Spring experiment) time before the start of the breeding season. For the Winter experiment, three-spined sticklebacks were captured with a dip net and minnow traps in the River Endrick, Scotland, UK (56°04′N, 4°23′W) on 1 November 2007. Fish for the corresponding Spring experiment were captured from the same location on 29 January 2008. On both occasions, all fish were initially transferred to acclimatisation aquaria (80 litres and density 2 fish l⁻¹) for 3 weeks and fed *ad libitum* with frozen chironomid larvae. The temperature was initially maintained at 9.7±0.1°C prior to the start of experiments, and the photoperiod was initially ambient.

#### Winter experiment

On 21 November 2007, fish for the Winter experiment were anaesthetised and standard length (±0.01 mm) and wet mass (±0.001 g) measured. Fish were then sorted into groups of five (of differing size, to aid identification; regular measurements throughout the experiment confirmed that size ranks never changed within a tank), with each group of five fish in a separate tank (335 mm×170 mm×185 mm). Each tank was provided with aeration, a filter and artificial plants. 25% of the total volume of water (1.75 litres) was changed every week. We also added 62.5 ml of seawater per tank to reduce the risk of whitespot infection *Ichthyophthirius multifiliis*. Four replicate tanks of five fish were assigned randomly to each of the three temperature manipulations: high (14°C), low (6°C) and intermediate (10°C). These temperatures were applied for a 4-week period (Period 1), following which all fish were transferred to 10°C (Period 2; Table 1). On 16 May, by which time males had started to develop their breeding coloration (reddish throats) and females to become gravid, the temperature was changed to 14°C to allow the fish to breed (Period 3). Food rations (chironomid larvae) were provided *ad libitum* once per day throughout the experiment.

In order to examine the extent to which an alteration in the perception of time of year (and hence time until breeding) influences the growth response, the above three groups were replicated under two different photoperiod regimes: the fish were either given the photoperiod treatment or were transferred to a day length which differed (i.e. high (14°C), low (6°C) and intermediate (10°C)). These temperatures were applied for a 4-week period (Period 1), following which all fish were transferred to 10°C (Period 2; Table 1). On 16 May, by which time males had started to develop their breeding coloration (reddish throats) and females to become gravid, the temperature was changed to 14°C to allow the fish to breed (Period 3). Food rations (chironomid larvae) were provided *ad libitum* once per day throughout the experiment.

#### Table 1. Description of temperature and photoperiod manipulations

| Group | Temperature manipulation | Photoperiod manipulation |
|-------|--------------------------|--------------------------|
| HTA   | High (14°C)              | Ambient                  |
| HTD   | High (14°C)              | Delayed (35 days)        |
| ITA   | Intermediate (10°C)      | Ambient                  |
| ITD   | Intermediate (10°C)      | Delayed (35 days)        |
| LTA   | Low (10°C)               | Ambient                  |
| LTD   | Low (10°C)               | Delayed (35 days)        |

Period 1: the 4-week manipulation period; Period 2: the compensatory period; Period 3: the breeding season.

LT, IT and HT: low, intermediate or high temperature; A, D: ambient or delayed photoperiod.

The entire experiment was run twice, with different fish, starting in November (Winter experiment) and February (Spring experiment). Fish were fed *ad libitum* throughout the experiment.
was 2 h longer at the start of the manipulation, corresponding to a point 35 days earlier in the autumn (the delayed photoperiod treatment). The photoperiod for all fish was achieved using fluorescent lights controlled by electronic timers, with blackout plastic sheeting around the tanks being used to achieve independent lighting regimes. The photoperiod in the ambient and delayed treatment groups then changed at the ambient and delayed (−35 days) seasonal rates of progression respectively, so that the photoperiod cue received by the fish in the delayed treatment would suggest that they were continually at a stage 35 days earlier in the season (i.e. initially late autumn instead of early winter), and thus had a longer growth period ahead prior to the breeding season.

Thus, overall within this Winter experiment there were six manipulation groups (three temperature × two photoperiod treatments, each with four replicate tanks), which enabled us to examine the effect of temperature-induced compensatory growth on swimming performance, and whether the magnitude of the response was influenced by perceived time until the breeding season. Since the intermediate temperature manipulation groups experienced no temperature change, being held at 10°C until the breeding season, we predicted that they would experience steady growth; the low temperature manipulation groups had a 4-week period at 6°C followed by 10°C, so were expected to show slowed growth followed by (compensatory) growth acceleration; and the high temperature manipulation groups were expected to show the opposite growth pattern (faster growth for 4 weeks followed by a deceleration). If the response of the fish was influenced by nearness to the onset of the breeding season, then we would expect fish in the delayed photoperiod manipulation groups to show weaker compensatory responses than their corresponding group exposed to an ambient photoperiod.

The length and mass of the fish were measured every 2 weeks during the temperature manipulations and every 3 weeks thereafter; all fish were starved for 24 h prior to measuring to prevent inflation of measured mass due to stomach contents. The length reached at the end of the temperature manipulation (i.e. Period 1) is referred to as the “manipulated fish length”. Tanks were inspected daily in order to monitor mortality rates throughout the experiment.

On 16 May, the fish were sexed on the basis of their coloration, and males that had developed the typical sexual ornamentation [blue eye coloration and red humps (Wootton, 1976)] were moved to individual tanks, which were of the same size and arrangement as their group tank but with the addition of a Petri dish containing fine sand (i.e. a nesting dish) and nesting material (50 × 5 cm lengths of thread). Once most males had built nests, each was shown a gravid female enclosed in a Plexiglas container for 5 min twice daily for 4 weeks to prompt full expression of nuptial coloration (Pike et al., 2007). Females were kept in their original group tanks and were stripped of clutches of eggs whenever they became fully gravid. Data on the effect of the experimental manipulations on reproductive performance will be presented in a separate paper.

Spring experiment
In order to examine whether the outcome was influenced by the stage the fish had reached when the experiment began, we repeated the above experiment using fish caught in early spring. In the Spring experiment the same process of measuring and assigning wild-caught fish to groups of five per tank was carried out on 21 February 2008, with four tanks being randomly assigned to the same six manipulations as before. All details of the experimental set-up were exactly as in the Winter experiment, except that this time the fish in the delayed photoperiod treatment were transferred to a day length which was initially 2 h shorter at the start of the manipulation, corresponding to a point 35 days earlier in the spring than the current date. The ambient photoperiod treatment fish experienced a photoperiod that tracked the natural seasonal progression, while the delayed photoperiod group experienced the same rate of change of the seasons except that it always appeared to be 35 days earlier in the year than was actually the case. Period 2 in the Spring experiment commenced on 20 March and Period 3 on 3 July, with males again being separated into individual tanks when they had developed signs of breeding coloration.

Analysis of growth rate
In order to compare the effect of growth rates between the two experiments, we calculated each fish’s relative growth rate, which controlled for seasonal and ontogenetic differences in growth rate between the experiments. We first determined the typical growth pattern for unperturbed fish during the compensatory period in each experiment, by using the data for the intermediate temperature group to regress gain in length over interval t on initial length $L_i$, both axes being on a logarithmic scale. The resulting regression equation for each experiment was then used to predict the expected growth during the compensatory period for all fish:

$$\ln[G_E] = m[\ln(L_i)] + c,$$

where $G_E$ is the expected gain in length over the compensatory period (Period 2) if no compensation occurred, $\ln(L_i)$ is the logarithm of initial length, and $m$ and $c$ are the regression parameters determined from the data for Intermediate temperature group. The relative growth rate was calculated as:

$$\text{relative growth rate} = \frac{\ln(G_{i1}) - \ln(G_{i2})}{\ln(G_{i1})},$$

where $G_{i0}$, the observed gain in length over the compensatory period, is given by $(L_{i0} - L_i)$. Mean values for relative growth rate were then calculated for each sex within each treatment group.

Swimming performance
We quantified swimming performance as the length of time a fish could swim against a constant strong current of water; this measure of swimming stamina has been used in previous studies (Ojanguren and Braña, 2000; Ojanguren and Braña, 2003; Royle et al., 2006) using several different species including sticklebacks (Álvarez and Metcalfe, 2005); the full details of the experimental setup are given elsewhere (see Álvarez and Metcalfe, 2005; Royle et al., 2006).

Swimming performance in both experiments was measured twice: (1) when fish in the different manipulation groups had finished the phase of compensatory growth and had converged on the same mean size prior to breeding; and (2) 18 weeks later (after the breeding season). The swimming trials were conducted inside a temperature-controlled room that maintained the temperature the same as in the holding tanks. One fish at a time was placed into a cylindrical swimming chamber (50 cm long, 20 cm diameter). The fish was initially subjected for 5 min to a moderate water velocity (17.0 cm s$^{-1}$) to allow it time to adapt to the apparatus. The water velocity was then increased to 34.9 cm s$^{-1}$ (slightly greater than the maximum that could be sustained by sticklebacks, based on pilot trials) and the time taken until fatigue was recorded. A fish was deemed to be exhausted when it was forced back against the fine mesh grid at the downstream end of the compartment for more than 5 s (Ryan, 1988) and was no longer able to continue swimming, despite our tapping the side of the chamber (Ojanguren and Braña, 2000). We immediately turned off the pump and the fish was allowed 5 min recuperation time before being measured (length and body mass)
and returned to its original tank. As a measure of recovery rate, we recorded the opercular ventilation rate (beats min⁻¹) during the 5 min recuperation time, and also recorded the time elapsed until the fish first began to move again. All fish quickly recovered and were swimming normally again within 2–5 min. Swimming endurance was defined as the amount of time that a fish swam at the highest flow rate. All experiments were performed under license from the UK Home Office.

Statistical analysis
We used multivariate analysis of variance (MANOVA) to test for differences in body length and mass at the beginning of each experiment, at the end of the temperature manipulation (Period 1), and t days later (see section on growth rates above), when fish in the different manipulation groups had apparently finished the phase of compensatory growth. The effect of manipulations on swimming endurance and recovery time was analyzed in both experiments using general linear mixed models (GLMM) with treatment (low, intermediate or high temperature, denoted LT, IT and HT, respectively), photoperiod (ambient or delayed) and sex (male or female) as fixed effects, tank as random factor to control for tank effects, and body length at the time of the first swimming test and breeding season growth (i.e. increase in length between the first and second swimming tests) as covariates, plus all interactions among variables. Temporal changes in swimming endurance and recovery time were calculated as the differences in values measured before and after breeding. To test the effect of relative growth rate on the change in swimming endurance over the breeding period, we used a general linear model (GLM) based on the mean value for each sex within each treatment group as data points, with change in swimming endurance as the dependent variable, sex and experiment (winter or spring) as factors and relative growth rate as a covariate. In all analyses non-significant variables were sequentially dropped from the analyses so that the final models only included significant terms. All means are presented with standard errors and all of the analyses were performed with SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

RESULTS
Compensatory growth response after temperature treatment
At the beginning of both experiments there were no differences in length or mass between the temperature manipulation groups [low temperature (LT), intermediate temperature (IT) or high temperature (HT); MANOVA, Winter: Wilk’s λ=0.954, $F_{4,232}=1.34$, $P=0.26$, Spring: Wilk’s λ=0.994, $F_{4,232}=0.17$, $P=0.96$], or between photoperiod treatments in each temperature group [ambient photoperiod versus delayed photoperiod (MANOVA, Winter: Wilk’s λ=0.990, $F_{4,232}=0.55$, $P=0.58$, Spring: Wilk’s λ=0.997, $F_{4,232}=0.19$, $P=0.83$)]. However, by the end of the temperature manipulation period (day 28, end of Period 1), there were significant differences in length and mass between temperature manipulation groups in both experiments (Winter: Wilk’s λ=0.867, $F_{4,232}=4.02$, $P=0.004$, Spring: Wilk’s λ=0.812, $F_{4,218}=5.82$, $P<0.001$; Fig. 1), whereas there were no effects of photoperiod on length or mass (Winter: Wilk’s λ=0.999, $F_{4,232}=0.04$, $P=0.96$, Spring: Wilk’s λ=0.977, $F_{4,218}=1.23$, $P=0.30$). In the Winter experiment, LT fish were 6.6% smaller in standard length (ANOVA, $F_{1,76}=4.67$, $P=0.034$) and 28.3% lighter in mass ($F_{1,76}=8.12$, $P=0.006$) than HT fish at the end of Period 1. Similarly, in the Spring experiment, at the end of Period 1 LT fish were 5.3% smaller in length ($F_{1,71}=3.68$, $P=0.059$) and 30.1% lighter in mass ($F_{1,71}=10.11$, $P=0.002$) than HT fish. In both experiments, IT fish were intermediate in size and mass between HT and LT fish.

During the 4-week period of temperature manipulation, the mortality in the Winter experiment was 0%, 10% and 10% for the LT, IT and HT temperature manipulation, respectively; there was no difference in mortality among treatments ($\chi^2=2.069$, d.f.=2, $P=0.36$). By contrast, there was a treatment effect on mortality in

Fig. 1. Growth trajectories (logarithm of standard length in mm and of wet mass in mg) of three-spined sticklebacks (*Gasterosteus aculeatus*) in the Winter (A,C) and Spring (B,D) experiments. Note that the two experiments started on different days, so that day 1 is 21 November in A and C and 21 February in B and D. The thick horizontal line indicates the period of temperature manipulation (28 days; triangle, 14°C; circle, 10°C; square, 6°C). After this period, the temperature for all three groups was kept at 10°C until the start of the breeding season (B), at which point the temperature was raised to 14°C and male sticklebacks were isolated from female sticklebacks (see Materials and methods for more details). ‘S1’ and ‘S2’ indicate the timing of the swimming trials (i.e. at the end of the period of compensatory growth and 18 weeks later, after the breeding season). Asterisks indicate significant differences among treatment groups ($P<0.05$).
the Spring experiment ($\chi^2=14.87$, d.f.=2, $P=0.001$). This was due to 35% mortality in the HT group as compared with zero mortality in the other two groups. This higher mortality (seven fish) in the HT group was almost entirely due to all five fish in one tank dying suddenly on 8 March 2008, for unknown reasons (all other mortality in the experiments was spread across tanks and days in no clear pattern). Note that the data for fish that subsequently died during the course of the study were excluded from all analyses, to ensure that none of the statistics on growth rate etc would be biased by any differential mortality rates.

The size differences did not persist once the fish were transferred to the same conditions (10°C) at the end of Period 1: compensatory growth occurred (in terms of both accelerated growth in LT groups and accelerated growth in HT groups, relative to IT fish) such that the growth trajectories of the different temperature treatment groups converged (Fig. 1). In the Winter experiment, the significant differences in size between temperature groups had disappeared 15 weeks after the end of the manipulation period (comparison of sizes at 15 weeks: Wilk’s $\lambda=0.946$, $F_{3,182}=1.29$, $P=0.28$); in the Spring experiment, the compensation was quicker and the corresponding time for size differences to disappear was 12 weeks (Wilk’s $\lambda=0.985$, $F_{3,180}=0.37$, $P=0.83$). Although growth rate during the compensatory growth (Period 2) was slower for delayed than for ambient photoperiod treatment fish in the Winter experiment (GLM, effect of photoperiod: $F_{1,95}=7.77$, $P=0.006$), there was no effect of photoperiod on growth rate in the Spring experiment ($F_{1,98}=0.63$, $P=0.431$).

**Swimming endurance**

Endurance was first measured when the fish from the different manipulation groups had approximately converged in mean size (i.e. growth compensation was complete). For the Winter experiment, endurance was measured an average of 114.5 (range 112–117) days after the end of the temperature manipulation, whereas for the Spring experiment the measurements were on average 93.5 (range 91–96) days after the manipulation had finished. At this first measurement of swimming performance there was no difference between temperature treatments in endurance in the Winter experiment (GLMM, $F_{2,91}=0.32$, $P=0.724$), but there was a significant difference in the Spring experiment, with HT fish having the greatest swimming endurance (Fig. 2; Table 2). In both experiments, photoperiod influenced endurance (the longest endurance being shown by delayed treatment fish) and there were positive effects of body length at the time of the swimming test on endurance (i.e. larger fish had greater endurance; Table 2). Sex did not influence pre-breeding swimming endurance directly in either experiment (Table 2). In the Spring experiment, there were significant interactions between temperature and photoperiod, and between photoperiod and body length at the time of the first swimming test: the effects of both temperature and body length were greater under the delayed photoperiod (Fig. 2 and Table 2).

When tested again at the end of the breeding season, the average swimming endurance of all categories of fish had declined. The within-individual change in endurance over the course of the breeding season was analysed using GLMM models, with the same terms as before plus breeding season growth as a covariate. The change in endurance did not differ between temperature treatment groups in the Winter experiment ($F_{2,85}=3.01$, $P=0.055$), but there was a significant temperature treatment effect in the Spring experiment: LT fish showed the biggest decline in endurance and HT fish declined least (Fig. 3; Table 3). In the Winter experiment, breeding season growth and the interaction between body length at the time of the first test and breeding season growth both influenced the change in swimming endurance (Table 3): the smallest decrease in endurance was shown by those fish that grew most during the breeding season, especially if they were amongst the largest at the start of the season. However, there were no significant effects of photoperiod, sex or other interactions on the change in swimming endurance (Table 3). In the Spring experiment, the change in swimming endurance over the breeding season was significantly influenced by body length at the time of the first swimming test:

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**Table 2. Results of general linear mixed model analyses examining initial swimming endurance in relation to temperature treatment, photoperiod treatment, sex and body length at the time of the test in the Winter and Spring experiments**

| Experiment | Final model                                      | $F$   | d.f. | $P$       |
|------------|-------------------------------------------------|-------|------|-----------|
| Winter     | Photoperiod                                     | 4.60  | 1, 91| 0.035     |
|            | Body length at first test                        | 102.99| 1, 91| <0.001    |
| Spring     | Temperature                                     | 5.61  | 1, 90| 0.005     |
|            | Photoperiod                                     | 5.27  | 1, 90| 0.024     |
|            | Body length at first test                        | 206.29| 1, 90| <0.001    |
|            | Temperature $\times$ photoperiod                | 7.77  | 1, 90| 0.001     |
|            | Photoperiod $\times$ body length at first test  | 5.31  | 1, 90| 0.024     |

Non-significant variables were sequentially dropped from analyses apart from main effects occurring in significant interactions. Tank was included as a random factor.
larger fish at the time of the first test showed less of a decrease in endurance (Table 3). There was also a significant interaction between photoperiod, sex and body length at the time of the first swimming test (Table 3). The patterns were therefore complex, but overall the decrease in endurance was greatest in females from the ambient photoperiod group that were smallest at the time of the first swimming test.

To summarise the trends across both experiments, we analysed the effect of relative growth rate (see Materials and methods) on the change in swimming endurance, using the mean value for each sex within each treatment group as data points (so N=2 sexes × 3 temperatures × 2 photoperiods × 2 experiments=24). The sexes were separated since there was a significant interaction involving sex and body size (see preceding paragraph) and females tended to grow more than males over the breeding season. The data were analysed by GLM, with change in swimming endurance as the dependent variable, sex and experiment (winter or spring) as factors and relative growth rate as a covariate. The estimated decrease in swimming endurance tended to be greater in males (–0.26±0.04) than in females (–0.16±0.04), but this effect of sex was marginal ($F_{1,24}=4.30, P=0.051$), so it was dropped from the model. The change in swimming endurance was negatively affected by relative growth rate (i.e. the faster the relative grow rate of a treatment group, the bigger the reduction in swimming performance over the breeding season; $F_{1,24}=14.85, P<0.001$). However, for a given rate of growth, the adverse effect on swimming was stronger in the Spring experiment (Fig. 4; $F_{1,24}=18.73, P<0.001$). The interaction between season of experiment and relative growth rate was not significant ($F_{1,24}=0.56, P=0.462$).

**Recovery time**

The final models analysing recovery time (after removal of non-significant terms) showed no effect of temperature treatment in the Winter experiment (GLMM $F_{2,96}=0.34, P=0.715$) but a significant effect in the Spring experiment, with LT fish taking longer to recover (Fig. 5; Table 4). In both experiments, there was a significant effect of photoperiod on recovery times, with fish in the delayed

### Table 3. Change in swimming endurance over the breeding season in relation to temperature treatment, photoperiod treatment, sex, body length at the time of the first swimming test and breeding season growth (i.e. length at the second swimming test – length at the first swimming test) in the Winter and Spring experiments

| Experiment | Final model | $F$  | d.f. | $P$ |
|------------|-------------|------|------|-----|
| Winter     | Body length at the first test | 1.59 | 1, 81.40 | 0.211 |
|            | Breeding season growth | 5.60 | 1, 83.79 | 0.020 |
|            | Body length at first test × breeding season growth | 5.45 | 1, 83.95 | 0.022 |
| Spring     | Temperature | 32.62 | 2, 14.75 | <0.001 |
|            | Photoperiod | 2.49 | 1, 58.48 | 0.120 |
|            | Sex | 1.32 | 1, 66.36 | 0.255 |
|            | Body length at first test | 3.53 | 1, 61.57 | 0.065 |
|            | Photoperiod × sex × body length at first test | 4.33 | 3, 65.96 | 0.008 |

Non-significant variables were sequentially dropped from analyses apart from main effects occurring in significant interactions. Tank was included as a random factor.
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Fig. 5. Mean ± s.e.m. recovery time (seconds; ln transformed) of three-spined sticklebacks after the first swimming endurance trial in relation to photoperiod treatment (ambient and delayed), measured after growth compensation in relation to temperature manipulation (low, intermediate and high). (A) Winter experiment; (B) Spring experiment. Data are expressed as in Fig. 2 – see text and Table 4 for analyses.

Fig. 6. Change over the breeding season in the time (seconds; ln transformed) taken by three-spined sticklebacks to recover from a swimming endurance trial, shown in relation to temperature treatment (low, intermediate and high). (A) Winter experiment; (B) Spring experiment. Data are expressed as in Fig. 2 and see text and Table 5 for analyses; positive values indicate that fish were slower to recover after the breeding season.

photoperiod treatment recovering fastest (Table 4). Although there was no effect of body length at the time of the first swimming test on recovery time in the Winter experiment, this term was significant in the Spring experiment, with larger fish recovering faster (Table 4). However, there was a significant interaction between photoperiod and body length at the time of testing in both experiments, with the slowest recovery being in shorter fish from the ambient photoperiod group (Table 4). In neither experiment did other interaction terms or sex have significant effects on recovery time (Table 4).

Recovery times tended to be longer when the fish were re-tested for swimming endurance at the end of the breeding season (Fig. 6). Using GLMM models, with the same terms as before plus breeding season growth as a covariate, we analysed the change in recovery time over the course of the breeding season. The change in recovery time did not differ between temperature groups in the Winter experiment ($F_{2,89}=0.41, P=0.665$), but it was significant in the Spring experiment, with HT fish recovering fastest (Table 5). The photoperiod treatment was significant in both experiments, with fish in the delayed photoperiod recovering fastest (Table 5). In the Winter experiment the change in recovery time was not affected by body length at the time of the first swimming test, whereas in the Spring experiment larger fish showed less of a reduction in recovery time (Table 5). An interaction between photoperiod and body length at the time of the initial test influenced the change in recovery time (Table 5), with larger fish in the delayed photoperiod group showing least increase in recovery time. There were significant effects of interactions between temperature and sex in the Winter experiment, and between temperature and body length at initial testing in the Spring experiment (Table 5): HT males and bigger HT fish showed least increase in recovery time, respectively. In neither experiment was the effect of sex significant.

**DISCUSSION**

Environmental temperatures in early life are known to exert strong effects on the life history of sticklebacks (Wootton, 1998). Our study found that a brief (4 week) period of manipulated temperature caused effects on growth trajectory not only during the manipulation itself (as would be expected for an ectotherm), but also on subsequent growth trajectories. The growth rates affected body length as well as body mass and so were not simply a change in levels of energy storage. Those fish experiencing the low temperature treatment would have grown slowly because of a reduction in the ability of the fish to process food and synthesise new tissues (Bone and Moore, 2007). When the temperature increased again they showed growth acceleration, whereas fish in the high temperature treatment showed a subsequent growth deceleration when returned to the intermediate temperature. These changes in growth were not simply a physiological response to the new temperature, since growth trajectories of the three treatment groups converged rather than ran parallel to each other, even though all were under the same environmental conditions at the time. The accelerated growth of the LT fish was presumably due to increased food consumption, which may have been at a level higher than would normally be expected for that temperature [i.e. hyperphagia, as has recently been shown in juvenile brown flounder *Paralichthys olivaceus* (Huang et al., 2008)]. Conversely, the HT fish may have exhibited a slightly suppressed food intake until their growth trajectory had converged with that of the IT fish as control fish. There was thus compensatory

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**Table 4. Recovery time after the first swimming test in relation to temperature treatment, photoperiod treatment, sex and body length at the time of the test in the Winter and Spring experiments**

| Experiment | Final model        | $F$  | d.f. | $P$  | $P$  |
|------------|--------------------|------|------|------|------|
| Winter     | Photoperiod        | 9.92 | 1, 90| 0.002|      |
|            | Body length at first test | 2.01 | 1, 90| 0.160|      |
|            | Photoperiod × body length at first test | 9.90  | 1, 90| 0.002|      |
| Spring     | Temperature        | 14.61| 2, 92| <0.001|      |
|            | Photoperiod        | 9.05 | 1, 92| 0.003|      |
|            | Body length at first test | 185.26 | 1, 92| <0.001|      |
|            | Photoperiod × body length at first test | 9.37  | 1, 92| 0.003|      |

Non-significant variables were dropped from the final model apart from main effects occurring in significant interactions. Tank was included as a random factor.
growth, in both directions, in fish that had earlier experienced a phase of fast or slow growth, even though none of the fish had experienced any food shortage at any time.

It has previously been shown that compensatory growth prompted by changes in nutrition may subsequently affect a range of fitness traits, including locomotor performance (Álvarez and Metcalfe, 2005; Álvarez and Metcalfe, 2007). The results of the present study support previous work showing that accelerated growth could result in costs to swimming performance in later life, especially if the growth acceleration occurred close to the breeding season (Álvarez and Metcalfe, 2005); in the present experiment, stronger effects of the same manipulation were found in the Spring than in the Winter experiment (see Fig.4), despite the fact that growth rates were similar. However, we also show for the first time that ‘negative compensation’ (i.e. a decelerating growth trajectory) led to an improved swimming performance compared to steadily growing controls. This beneficial effect of a decelerating growth trajectory on both swimming (shown here) and reproductive investment (W.-S.L., P.M. and N.B.M., unpublished) may explain why such fish showed a reduced growth rate despite other advantages of larger size during the upcoming breeding season. Swimming capacity in fish is affected by body size and muscle energy reserves (Guderley, 2004), but given that there was no difference in body size or nutrition between treatment groups at the time of testing, the treatment effects on swimming performance may instead be related to muscle structure. It is well known that accelerated growth negatively affects muscle cellularity and development (Galloway et al., 1999; Johnston et al., 2002). The development of new muscle fibres is constrained during ontogeny: for instance, the number of fast muscle fibres reaches an asymptote before the fish is half its size at sexual maturity, so that subsequent increases in the size of the muscles can only be achieved by expansion of existing muscle fibres (Johnston, 2006). Differences in the timing of muscle fibre recruitment during development have been shown to lead to different compositions of white and red muscle fibres (Johnston, 2006): for instance, fast-growing fish have higher percentages of small-diameter white muscle fibres and greater numbers of similar-diameter red muscle fibres than slow-growing fish (Valente et al., 1999). Such growth-induced differences in muscle structure have been shown in herring (Clupea harengus) to translate into differences in swimming performance that persist even when fish are subsequently growing at the same rate (Johnston et al., 2001). Effects of embryonic conditions on muscle development and subsequent motor performance are not restricted to fish: effects of early growth rate on tail muscle fibre numbers and swimming performance have been found in tadpoles of both toads (Arendt and Hoang, 2005) and frogs (Watkins and Vraspir, 2006), and it has been suggested that such a trade-off between early growth rate and locomotor performance is common to all vertebrates (Arendt, 2003).

The acceleration of growth induced by the LT regime might also have increased the level of damage incurred during development of myotomal muscle, for instance, through higher levels of oxidative stress. Recently Pike et al. (Pike et al., 2007) showed that growing sticklebacks that had a reduced access to dietary antioxidants were less able to invest in defence against oxidative stress, which can cause damage to a wide range of biomolecules. The modification of anabolic processes that allow an acceleration of tissue growth may involve a diversion of resources towards the synthesis of new protein and away from repair of existing tissues (Morgan et al., 2000). Fish on the LT regime might therefore accumulate more damage, leading to impaired muscle function, whereas those experiencing a decelerated growth trajectory (HT fish) might have been able to invest proportionally more resources into repair (even more than the IT fish) and so would have a lower level of damage. Such effects were not restricted only to the time fish were able to swim against a strong current, since the recovery time was longer in accelerated than decelerated growth groups, even though they had spent less time swimming.

The effects of growth trajectory on locomotor performance were evident at the time of the first swimming trial at the end of the compensation period, but they were amplified later in life, after the breeding season. The breeding season for three-spined sticklebacks lasts from late April until July or August: during this time females produce a sequence of clutches of approximately 100 eggs which they lay in nests that are built by males, who then provide all the care (e.g. nest aeration by fanning, defence against predators and cannibals) for the eggs and young fry (Wootton, 1976). The breeding period is thus costly for both sexes (Pike et al., 2007). Similar reproductive costs have been shown to include a temporary impairment of locomotor abilities during the breeding season across a range of organisms [e.g. whelks (Brokordt et al., 2003); passerine birds (Lee et al., 1996; Veasey et al., 2000; Kulberg et al., 2002)]. In the present study all groups showed on average a poorer swimming endurance (coupled with a slower recovery) after the breeding season, but this was accentuated in the groups that had earlier exhibited the fastest growth rate. Therefore the cost of accelerated growth lasted well beyond the time over which growth rates differed between treatment groups.

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Table 5. Change over the breeding season in time to recover from a swimming endurance trial, in relation to temperature treatment, photoperiod treatment, sex, body length at the time of the first swimming test and breeding season growth (i.e. change in length between the first and second swimming tests) in the Winter and Spring experiments

| Experiment | Final model                              | F    | d.f. | P      |
|------------|------------------------------------------|------|------|--------|
| Winter     | Temperature                              | 0.41 | 2, 80 | 0.665  |
|            | Photoperiod                              | 9.06 | 1, 80 | 0.003  |
|            | Sex                                      | <0.001 | 1, 80 | 0.976  |
|            | Body length at first test                 | 1.18 | 1, 80 | 0.280  |
|            | Temperature × sex                        | 4.18 | 1, 80 | 0.019  |
|            | Photoperiod × body length at first test   | 8.96 | 1, 80 | 0.004  |
| Spring     | Temperature                              | 6.69 | 2, 80.70 | 0.002 |
|            | Photoperiod                              | 8.86 | 1, 80.52 | 0.004 |
|            | Body length at first test                 | 17.84 | 1, 80.52 | <0.001 |
|            | Temperature × body length at first test   | 6.95 | 2, 80.80 | 0.002 |
|            | Photoperiod × body length at first test   | 8.97 | 1, 80.40 | 0.004 |

Non-significant variables were dropped from analyses apart from main effects occurring in significant interactions. Tank was included as a random factor.
The prevailing photoperiod can influence the time available per day for feeding activity, and so can affect growth rate. However, it also indicates the time of year and hence time available before key life history events. The ‘time-stress’ hypothesis (Metcalfe et al., 2002) suggests that animals should be sensitive to the amount of time available when altering their growth trajectory to compensate for a period of perturbed growth, showing a stronger compensation (and hence potentially greater long term costs of compensation) when the time until an approaching life history event, such as reproduction, was shorter. Our results provide strong support for the hypothesis. Firstly, the effect of the temperature treatment was much stronger in the Spring experiment, where the time available from the end of the manipulation until the breeding season was shorter. Secondly, although the photoperiod manipulation with the Winter and Spring experiments had little effect on growth rates during the compensation period, it did affect initial swimming endurance, recovery time and the change in recovery time over the breeding season. In each case the fish that perceived a greater time from the temperature manipulation until the breeding season (i.e. the delayed photoperiod group) showed the better performance. Given that there was no effect of the photoperiod manipulation on growth rates, these effects on swimming performance may have been due to differential investment in somatic repair: the delayed photoperiod groups would have had a longer time in which to repair any damage in the run up to the breeding season, and may have had a different balance of investment between somatic repair and gonad growth, hence a slower accumulation of cellular damage (Jennings et al., 2000). However, this remains speculation at this stage without further detailed study.

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