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Temperature Acclimatisation of Swimming Performance in the

European Queen Scallop

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Abstract

The phenotypic plasticity of the muscle performance and locomotory physiology of a wide phylogenetic range of eurythermal vertebrates allows the maintenance of essential activity capacity in the face of environmental change. This study used the scallop, *Aequipecten opercularis*, as a model eurythermal invertebrate. Animals caught in different seasons demonstrated marked differences in their swimming performance and the relationship between temperature and performance. When stimulated to swim at natural ranges of temperature, Winter (cold acclimatised), animals accelerated faster than Autumn collected animals swimming at the same temperature (x2 at 11°C) and attained higher velocities during jetting. The effects of acclimatisation were confined to the jetting phase and may be a mechanism for the maintenance of acceleration during predator-prey interactions. This is the first demonstration of the thermal acclimatisation of muscle performance in a mollusc and one of very few studies in invertebrates.

Keywords: Swimming, temperature, acclimatisation, phenotypic plasticity, muscle, invertebrate, scallop, Pectinidae, *Aequipecten opercularis*.

1. Introduction

In many species, the effects of temperature on activity vary following several weeks acclimation to a new temperature regime in the laboratory or with seasonal acclimatisation in the field (Hazel and Prosser, 1974; Johnston and Temple, 2002). Improvements in whole-body performance and associated changes in physiology following temperature acclimation have been shown in numerous species including temperate fish (Heap and Goldspink 1986; Johnston et al. 1990; Johnson and Johnston 1991), and crabs (Pearson et al. 1999). Temperature acclimation responses are most likely to evolve in a species if the changes required are energetically cheap, the environment is variable, and selection favours plasticity equally strongly amongst equally common conditions (Scheiner 1993; Angilletta et al., 2003). A cue must be present that correlates to the strength of the selective advantage of plasticity. If these conditions do not apply then a generalist strategy is favoured (Scheiner 1993). Examples of species which show little or no change with acclimation include Antarctic fish (Hardewig et al. 1999), which are subject to very small temperature fluctuations, and salamanders, which lack a reliable cue (Else and Bennett 1987).

The European Queen Scallop, *Aequipecten opercularis* may meet the criteria for the evolution of an acclimatory response. The thermal environment inhabited by the species is variable temporally with the seasonal changes being both predictable and associated with a strong photoperiod cue. In *Placopecten magellanicus*, a scallop with similar predators and temperature range to the study species, the use of jet propelled swimming (Cheng et al. 1996) appears to be important in surviving predator-prey interactions, with the effectiveness of escapes depending on environmental temperature (Barbeau and Scheibling 1994b; Barbeau and Scheibling 1994c). It seems likely then that both escape performance and its relationship to water temperature may be subject to selective pressure.

2. Methods

2.1. Animals

300 *Aequipecten opercularis* were obtained from Loch Fyne Seafarms in November 1999 and February 2000. Water temperatures at the open-water Seafarms site for the month prior to each collection were determined as $13 \pm 3^{\circ}\text{C}$ and $8 \pm 2^{\circ}\text{C}$ (mean \pm range) respectively using temperature loggers (TinyTalk

loggers, RS Electronics, UK) deployed at the same depth as the scallops. Scallops were maintained at their mean monthly temperature ($\pm 0.3^{\circ}\text{C}$) in a purpose built temperature controlled tank (3m x 1m x 0.3m, length x width x height) under a 12h light:12h dark regime for 48 h before beginning experiments. Mean shell height was 56.7 ± 0.73 mm (± 1 s.e.) and did not differ significantly between groups.

2.2. *Filming*

Scallops were stimulated to swim by touching a dissected starfish (*Asterias rubens*) limb to the scallop's mantle tentacles close to the hinge. The resulting escape responses were recorded at 250 Hz by a high-speed video system (NAC HSV500c³, NAC Inc. Japan). The camera was mounted on a tripod and faced the long side of a glass swim tank (0.8 x 0.4 x 0.4 m) at a range of three metres. Animals were moved into the swim tank and allowed to rest for a minimum of 2 h before the first escape response was stimulated.

Filming was completed within 2 weeks of the arrival of the animals in the laboratory. Field acclimatised animals were swum anywhere within the temperature range recorded at the sample site for the month prior to sampling (Autumn, 8.7-16 $^{\circ}\text{C}$, mean 12.5 $^{\circ}\text{C}$, Winter 6-12.6 $^{\circ}\text{C}$, mean 9.7 $^{\circ}\text{C}$).

2.3. *Analysis of swimming*

Video recordings of the first "clap" of escape responses were played frame-by-frame on a PC. Only swimming responses were analysed, defined as the animal going on to make one or more further adductions while clear of the floor of the tank. Points on the valves were digitised in order to determine the animal's shell gape, while displacement of the hinge was used to calculate total velocity (U , $\text{m} \cdot \text{s}^{-1}$) and total acceleration (A , $\text{m} \cdot \text{s}^{-2}$). Maximum and mean values over the entire first cycle are denoted by the subscripts _{max} and _{mean}. The mean swimming velocity during the jetting phase (while the shell was closing) is denoted by U_{jet} ($\text{m} \cdot \text{s}^{-1}$).

3. Results

3.1. Effects of seasonal acclimatisation on swimming

The swimming performance of scallops acclimatised to different temperatures in the field were compared over a range of temperatures. Representative clap cycles at a common temperature (11°C) are presented in Fig 1. In this case the winter animal was swimming above its mean acclimatisation temperature and the autumn animal below its mean acclimatisation temperature.

Each clap cycle consisted of the scallop closing and then re-opening its shell. Initial closure was rapid but declined in rate during closure, this was immediately followed by a faster shell opening phase. The form of the clap cycle was modified by temperature change and differed according to the season of collection (Fig. 1). Winter animals completed the closing phase of the clap cycle significantly sooner (ANCOVA, $p = 0.012$, $df = 16$) than autumn animals, and had lower clap durations (Fig 2).

Swimming velocity (U , $m \cdot s^{-1}$), increased rapidly as closing began to a peak value after 0.1-0.15s. The animal then decelerated slowly after the end of valve closure before decelerating rapidly after valve reopening (Fig. 1). Peak total acceleration (A) and \dot{U}_{jet} were significantly higher in winter than in autumn animals (Fig 3) while U_{max} and U_{mean} did not differ significantly (Fig 3). U_{jet} was significantly related to temperature in both groups (Fig. 3) Gains in performance at higher temperatures occurred early in the cycle and were derived from the shortening in the duration of jetting. Winter animals swam in a much more jerky manner with U_{max} significantly higher for the same U_{mean} in autumn acclimated animals (t-test, $p < 0.001$, $df = 16$).

4. Discussion

4.1. Effects of field acclimatisation on swimming

Whole-body and muscle performance characteristics differed between animals acclimatised to winter and autumn conditions in the field when swum at similar temperatures. Cold acclimated animals accelerated faster and attained higher mean speeds during jetting than warm acclimated animals of the same population, when swimming at the same temperature. Velocity and acceleration during jetting were significantly related to temperature. However, as the duration of jetting reduced with increasing temperature this did not translate into large changes in swimming velocity integrated over

the cycle as a whole. Changes in swimming performance between animals acclimatised to different seasons were therefore apparent in the temperature sensitive fraction of the scallops' swimming with, little difference between seasons in the temperature independent phases, controlled by the action of the hinge ligament.

Changes in muscle performance cannot be ascribed to reproductive conditioning as, although this process greatly affects scallop muscle recovery from exercise no changes in actual performance could be detected (Guderley et al. 1995; Boadas et al. 1997; Brokordt et al. 2000). Preparation for the summer reproductive season may reduce muscle mass in this species (Allison 1994). A small (7 %) reduction in mean wet muscle mass occurred between samplings, making the maintenance of performance in the winter acclimatisation group even more striking.

4.2. Fitter without being faster?

The adaptive significance, if any, of the changes in performance observed with acclimatisation in these scallops is not clear. In fish (Beddow and Johnston 1995), tadpoles (Watkins 1995) and snakes (Jayne and Bennett 1990), the importance of burst speed in predator-prey interactions has been demonstrated. This is by no means a universal rule. The importance of absolute swimming speed is likely to be greatest where predator and prey are closely matched in ability and much reduced where the predator is much faster than the prey (Arnott et al. 1998) or here, where the predators from which the scallop can normally escape are slow moving invertebrates such as seastars (Barbeau and Scheibling 1994a). In shrimp, timing and the angle of lateral movement is more important in encounters with fish than the velocity attained (Arnott et al. 1998). In scallops acceleration and thrust from the jets provide the impetus to break free of a predator and escape and are therefore most likely to be important, with the requirement to gain sufficient speed (and therefore lift) to sustain swimming following. However, without more information on the physics of predator-prey interactions it is not possible to evaluate this further. In order for the increase in thrust observed in cold acclimatised animals to be of adaptive significance it would have to demonstrably increase survival in actual encounters between scallops and their predators. Clearly it is important to understand the context under which muscle performance is utilised - in order to determine its adaptive significance.

Temperature compensation of muscle performance has been demonstrated widely (Bullock 1955; Heap and Goldspink 1986; Beddow et al. 1995; Temple and Johnston 1998), and some of the mechanisms elucidated including altered expression of myofibrillar proteins, ion pumps and metabolic enzymes (Johnston et al., 1975; Heap et al. 1985; Goldspink et al. 1992; Johnson and Bennett 1995; Ball and Johnston 1996 Johnston and Temple, 2002). Whilst it has often been assumed that improved locomotory performance following temperature acclimation is associated with some fitness benefit, the so-called “beneficial acclimation hypothesis”, this has not been conclusively demonstrated. Indeed, several alternative hypotheses to explain the adaptive significance of temperature acclimation responses have been proposed Huey and Berrigan, 1996). Tests of these hypotheses involving growth in bacteria, territorial defence in dragonflies and parasitism in apple moths (reviewed in Huey et al., 1999) have found that the beneficial acclimation hypothesis was supported less often than previously supposed. Thus whilst fitness benefits associated with the seasonal acclimatisation of swimming activity are plausible this remains to be tested empirically.

4.3. Conclusions

The swimming behaviour of freshly caught scallops differed according to their season of collection. Winter collected scallops demonstrated higher swimming velocities during jetting, and higher accelerations at winter temperatures, than scallops caught in November when the temperature in the field was higher. While these aspects of locomotion are of potential selective importance further study is required to determine the exact performances required during predator-prey interactions before this can be evaluated further.

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Fig 1A) Normalised shell gape plotted against time in representative Autumn (solid line, —) and Winter (dotted line, ·····) acclimatised European Scallops at 11°C. Although both cycles took place at the same temperature the clap cycle was of reduced duration in the winter animal as a result of the reduced time taken to complete shortening.

B) Swimming velocity (U , $\text{m} \cdot \text{s}^{-1}$) plotted against time in representative Autumn (13°C) and Winter (8°C) acclimatised animals swimming at 11°C. The Winter acclimatised animal (dotted line, ·····) was swimming above its normal temperature and accelerated earlier reaching peak velocity (U_{max}) earlier than the autumn acclimatised animal (solid line, —). In this case U_{max} was also higher.

Fig. 2. Clap duration (s) against temperature in autumn (closed circles, ●) and winter (open circles, ○) acclimatised animals. Clap duration reduced with increasing temperature in both Autumn and Winter animals. Dashed lines are 95% Confidence Intervals. Autumn, $y = 0.54x - 0.02$, $r^2=0.79$, $p<0.001$, $df=31$. Winter, $y = 0.69x - 0.03$, $r^2=0.87$, $p<0.001$, $df = 36$. The lines were significantly different (ANCOVA, $p < 0.001$, $df = 68$).

Fig 3A) Peak acceleration (A , $\text{m} \cdot \text{s}^{-2}$) against temperature in Autumn (closed circles, ●) and Winter animals (open circles, ○). A increased significantly with increasing temperature in both groups. Dashed lines are 95% Confidence Intervals. Winter, $y = 1.79x - 6.46$, $r^2=0.56$, $p=0.006$, $df=9$. Autumn, $y = 0.950x - 3.58$, $r^2=0.48$, $p=0.008$, $df=12$. The lines were significantly different (ANCOVA, $p=0.002$, $df=16$).

Fig 3B) Mean swimming velocity during jetting, (U_{jet} , $\text{m} \cdot \text{s}^{-1}$) in winter (open circles, ○) and autumn (solid circles, ●) acclimated animals. The period of jetting was defined as the period from the beginning of the first movement of the valves shell closure. Peak swimming velocity was typically attained at the end of this period. U_{jet} increased with increasing temperature in both groups though this was not significant in winter animals. Dashed lines are 95% Confidence Intervals. Autumn animals, $y = 0.015x + 0.0345$, $r^2 = 0.46$, $p = 0.02$, $df = 10$. Winter animals, $y = 0.012x + 0.188$. $r^2 = 0.23$, $p = 0.19$, $df = 8$. The groups were significantly different (ANOVA), $p=0.007$, $df=19$, $F = 9.18$.

Fig. 3C) Mean cyclic swimming velocity, U_{mean} , in winter (open circles, o) and autumn (solid circles, ●) acclimatised animals. U_{mean} did not increase significantly with increasing water temperature in either group. There was no significant difference between groups. U_{mean} may be higher than U_{jet} , especially in Autumn animals where the glide period (where velocity was relatively high) was prolonged. U_{mean} depended on both performance during jetting (which increases with temperature) and the length of time before opening the shell for the next cycle (which decreased with temperature).

Fig. 1A.

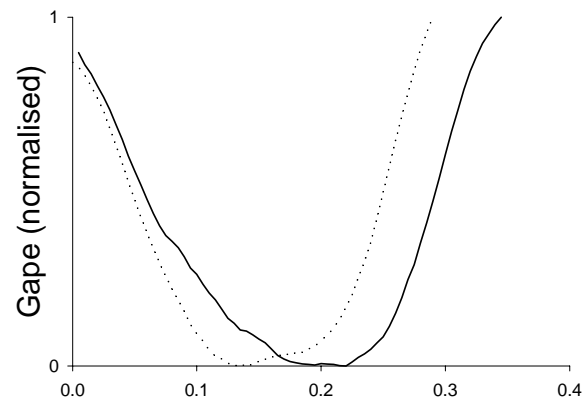


Fig. 1B.

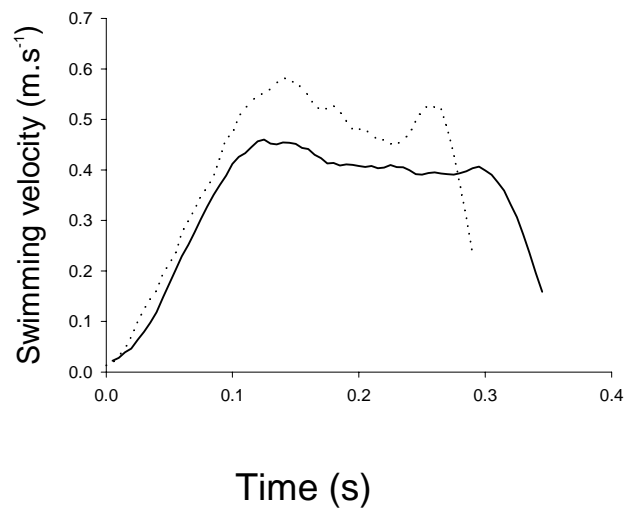


Fig. 2.

