Invertebrate muscle performance at high latitude: swimming activity in the Antarctic scallop, *Adamussium colbecki*.

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Abstract The escape swimming performance of the Antarctic scallop, *Adamussium colbecki*, was measured in animals acclimated for 6 weeks to –1°C, 0°C or 2°C and tested at –1.5°C to +1.5°C. Clap duration and swimming velocity were significantly related to temperature, but were not affected by acclimation, demonstrating no phenotypic plasticity. Comparisons of the mean swimming velocity of *A. colbecki* with published data for temperate and tropical species showed little evidence for evolutionary compensation for temperature, with all data fitting to a single exponential relationship with a Q_{10} of 2.08 (0-20°C). The contraction kinetics of the isolated fast adductor muscle of *A. colbecki* were determined and the times to 50% peak tension and 50% relaxation had Q_{10}s (0-4 °C) of 3.6 and 4.7 respectively. The Q_{10} of the overall relationship for pooled time to peak twitch data for 4 scallop species was 2.05 (0-20°C). Field studies revealed low mobility and poor escape performance in wild *A. colbecki*. A combination of thermodynamic constraints, reduced food supply, and lower selective pressure probably explains the low levels of swimming performance seen in *Adamussium colbecki*.

Introduction

Burst locomotor capacity typically defines one limit to an animal's performance envelope, being characterised by high velocities and accelerations of short duration (Beamish 1978). The intuitive links between burst performance and success in predator-prey interactions provide the potential for making ecologically relevant measurements of animal performance. Escape performance has been demonstrated to be crucial to survival (Watkins 1995), and to evolve rapidly in response to changing predation pressures (O'Steen et al. 2002). However, polar fish exhibit lower burst swimming speeds (Wakeling and Johnston 1998) and *in vitro* muscle performances (Johnston and Altringham 1985) than warmer-water species, but have similar abilities to recover from exercise (Hardewig et al. 1998). While temperature is known to have powerful effects on physiological processes, the effects of temperature-related changes in muscle performance on the survival and behaviour of fauna are not clear. Are the observed trends a result of a fundamental controlling influence of temperature on muscle performance, or does the selective advantage of high activity change at lower temperatures and/or higher latitudes?

Although polar fishes have been extensively studied, few experiments have been carried out on the burst performances of other cold-water animals (Ansell et al. 1998). Comparisons of findings in a distantly-related taxon should be useful in determining the factors controlling performance in polar animals. Like fish, scallops have a differentiated mass of fast-twitch muscle that is used mainly for burst swimming, and the importance of swimming performance to survival in scallops has been clearly demonstrated (Barbeau and Scheibling 1994a; b; c).

Adamussium colbecki (Smith 1902) is the only species of scallop extant in Antarctica, and has a circum-polar distribution with high local abundances (Berkman 1988). This species has been extensively studied and has a relatively high growth rate for an Antarctic mollusc (Berkman 1990; Brey and Clarke 1993), combined with a low basal metabolism (Heilmayer and Brey 2003). As for some polar fishes, *A. colbecki* demonstrates some temperature compensation for recovery from anaerobic exercise at its normal habitat temperature (Bailey et al. 2003), but rapidly loses the ability to swim as temperature increases (Peck et al. 2004). These scallops have been observed to swim readily in the wild (Ansell et al. 1998), but the effects of temperature on swimming performance in *A. colbecki* are unknown and no detailed comparisons exist between the swimming performances of this species and warmer-water scallops.

The main aim of the present study was to utilise quantitative measures of swimming and muscle performance, at a range of temperatures, in order to determine the effects of temperature on burst swimming over a range of timescales. Field experiments on the swimming of scallops, and on natural predator pressure, allowed the relative importance of physiological and ecological variables on swimming in scallops to be investigated.

Materials and methods

Study population

The scallops *Adamussium colbecki* were located in an area approximately 30 m across at 20-28 m depth and a smaller group at 12 m depth on an artificial boulder slope in North Cove, Rothera Point, Adelaide Island (67^{o}34’ S, 68^{o}08’ W). Most individuals were attached by byssal threads to rocks. All sites in the area were ice-impacted, and soft bottom areas around the boulder slope were dominated by the infaunal bivalve *Laternula elliptica*. Predators such

as the nemertean *Parborlasia corrugatus*, starfish *Odontaster validus* and the gastropod *Neobuccinum eatoni* were present.

Swimming activity in wild animals.

In situ, attached scallops were stimulated to attempt escape swimming in order to determine whether the attached animals could break free of the bottom. Homogenised seastar (*Odontaster validus*) or cold fresh water was squirted over scallops *in situ* (n = 7), and the resulting behaviours were recorded. These stimuli reliably produced escape responses in *A. colbecki* in the laboratory and are, respectively, a known predator of *A. colbecki* and a simulation of hyposaline lens encroachment, an observed trigger for swimming in wild populations (Berkman 1988).

Fifteen scallops were collected from the general population, marked with numbered foil patches, and placed on a level, rock surface (50cm x 120cm) at 8.5 m depth. The site was chosen to give a degree of protection from the North (main direction of iceberg approach) but was otherwise open. This site was visited 24 h after placement of the animals and then weekly for 2 months. The presence of byssus attachments and the distance moved by each animal was recorded.

Laboratory experiments

Scallops were collected using SCUBA and divided into three acclimation groups (n = 9) of the same mean shell height (67.2 ± 1.5 mm, mean ± 1 s.e.). The groups were maintained at –1 (±0.2), 0 (±0.5^{o}C), and 2^{o}C (±0.3) (mean ± range) in the controlled temperature room of the Bonner Laboratory, Rothera for 6 weeks prior to experimentation. This temperature range is similar to the seasonal variation at the study site (Peck et al. 2004). Attempts to acclimate *A. colbecki* to 5^{o}C failed, as did a following attempt at 4^{o}C, due to the rapid loss of

responsiveness and subsequent mortality in the groups before the end of acclimation (50% mortality in 14 and 19 days respectively). Animals were maintained in 30 l temperature controlled recirculating seawater aquaria (Grants, Cambridge) with water aeration by independent electric pumps. A constant low-light regime was maintained in order to mimic the Antarctic summer conditions. Limitations on space and equipment prevented the use of replicate tanks.

A further 20 animals were collected immediately prior to the end of the field season (04/03/99) for muscle performance experiments in the UK. These animals were maintained at in 0.40 m^3 aerated recirculating seawater tanks while being transported by ship and subsequently in the aquarium in St. Andrews, UK. Constant very low light conditions were maintained in order to mimic, as far as practicable, Antarctic marine winter conditions at 25-30 m depth.

Filming

The first clap cycles of *A. colbecki* escape responses were recorded on video at 25 frames $\cdot s^{-1}$ (Panasonic WVP-F10E camera with WV-LZ14/8AFE 8x Auto Focus Power Zoom Lens). 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. Twin 100W Spotlights were mounted on a second tripod 1 m from the tank providing illumination at approximately 45^o to the line of sight of the camera. Full details have been provided previously (Bailey 2001).

Animals were moved into the swim tank in groups of 4-5 animals from the same acclimation group. Animals were allowed to rest for a minimum of 6 h before the first escape response was stimulated. This rest period was the maximum time to 90% recovery recorded in this species following exhaustive exercise (Bailey et al. 2003). All acclimated animals were filmed.

Escape responses were stimulated using freshwater at (or as close as possible to) tank temperature. Water was introduced to the rear of the animal, directly beneath the hinge, using a tube attached to a 20 ml syringe. Typically 10 ml was injected at approximately 2 ml $\cdot s^{-1}$. There was minimal disturbance of the water around the animal and no force was exerted on the body of the scallop itself. The area of reduced salinity visible around the animal typically dispersed before adduction. Animals were used in rotation with a minimum of 2 h between stimulations.

Animals were swum initially at their acclimation temperature or the local water temperature at the time of the experiment, as appropriate. The swim tank temperature was then varied over a $-1.5^{O}C$ to $1.5^{O}C$ range to compare acute responses. Temperature changes were made in $0.5^{o}C$ increments at a maximum rate of change of $1^{o}C \cdot day^{-1}$ and no individual animal was exposed to a temperature of greater than $2^{o}C$ above or below its maintenance temperature.

Video sequences of the first clap of escape swimming were re-recorded onto Umatic video tapes (50 fields $\cdot s^{-1}$) and played back field by field using a PC (Gateway 2000 G6-266) with a video capture board (Hauppauge Win/TV). In each field the x and y co-ordinates of the scallop hinge were recorded using a program in Visual Basic 4.0 (Microsoft, USA). Swimming speed in the x and y directions were calculated from the displacement of the hinge, with total swimming velocity being the resultant. Mean cyclic swimming speed was calculated for the first clap cycle of escape responses.

In vitro muscle twitch characteristics

Experiments on isolated muscle fibres were carried out at the Gatty Marine Laboratory, St. Andrews in June 1999, approximately 1 month after the arrival of the scallops in the UK.

The ventral portion of the shell was cut back using a diamond edged circular saw blade on a variable speed electric drill (RS electronics, UK) exposing the adductor still attached to both valves. The majority of the adductor and other soft tissues were then dissected away to leave a small (<5 mm diameter) bundle of fast muscle fibres attached to the valves. The muscle preparation was then removed from the valves with pieces of shell (~ 25 mm^2) still attached to the ends. Foil hooks were attached to the ends of the muscle preparation for connection to the force and length transducers. The preparation was then further dissected in oxygenated ice-cold scallop Ringer (Olson and Marsh 1993) and attached to the transducers in the muscle chamber. Once placed within the apparatus each preparation was allowed to rest for 1 hour in oxygenated, re-circulating Ringer before experimentation. Temperature control was provided (±0.2^oC) by a pair of thermocirculators (Grants, Cambridge), cooling the oxygenated ringer and the jacket surrounding the system.

Stimuli were delivered by a pair of platinum wire electrodes and the force developed was detected by a silicon beam force transducer (AME 801, Senso-Nor, Norway). A LabView (National Instruments) program on a desktop PC (Elonex PC-433) with a LabPC Plus data input/output board (National Instruments) controlled the stimulator and captured the resulting force data.

Muscle preparation length was adjusted and single stimuli delivered in order to find the optimum length (L_{opt}) for twitch force production. Stimulus amplitude and pulse width were then optimised in turn. Following optimisation twitch experiments were conducted (40 V, 2 ms stimuli) and the temperature of the ringer was adjusted over the range 0-5^oC. Chamber temperature was returned to zero and the initial twitch repeated hourly in order to check for deterioration of the muscle preparation. No changes in twitch properties (time to max twitch or force production) at L_{opt} were observed, even after several hours. The cross-sectional area of the preparation was calculated from its mass, length and an estimated density of 1060 Kg · m^{-3} (James et al. 1998).

Results

Field studies of activity

When stimulated by homogenised seastar or freshwater, all 7 animals attempted to swim (several rapid adductions) but were unable to break the byssal threads attaching them to the rocks. The 15 marked scallops placed in the field remained attached to the rock in the original place 24 h later. During the 2 months of observation a boulder disturbed by ice impact landed on the site and killed 3 animals. No movement or mortality was observed amongst the remaining 12 animals.

The effects of temperature on swimming performance

Swimming responses in *Adamussium colbecki* consisted of a rapid closing phase (adduction), a glide phase, followed by reopening, as described previously in this species (Ansell et al. 1998). Both clap period and mean cyclic swimming speed were significantly related to temperature (Fig. 1 and 2). Differences between acclimation groups were investigated by ANOVA (with temperature as a covariate) and comparison of estimated marginal means and their 95% confidence intervals (SPSS ver. 12, SPSS Inc.). The overlap between the 95 % CIs indicated a lack of difference at the $p<0.05$ level. There were no differences in either of the above performance measures between acclimation groups when temperature was taken into account or for peak acceleration or peak velocity. The subsequent analyses were performed on pooled data for the groups combined.

Mean cyclic swimming velocities were compared between *A. colbecki* (this study), *Aequipecten opercularis* and *Zygochlamys patagonica* (Bailey 2001), *Placopecten magellanicus,* (Manuel and Dadswell 1990; Cheng and Demont 1996) *Argopecten irradians* (Marsh et al. 1992) and *Amusium pleuronectes* (Morton 1980), all swimming at natural

temperatures (see legend for animal sizes). A single exponential function described the effects of temperature on mean swimming velocity in all species reviewed here (Fig. 2), over a wide thermal range (-1.5 to 20^{o}C). The Q_{10} for the overall relationship was 2.08.

Muscle twitch characteristics

Time to peak muscle force development and time to 50% relaxation were recorded for 5 animals over the temperature range 0-5^{o}C. Contraction and relaxation durations decreased significantly with increasing temperature (time to peak twitch (ms) = 235.3 – temperature (^{o}C) · 25.9, r^2 = 0.52, p <0.001, df = 29; time to 50% relaxation (ms) = 567.9 – temperature (^{o}C) · 73.8, r^2 = 0.64, p <0.001, df = 29). The corresponding Q_{10}s (0-5^{o}C) were 3.6 and 4.7. Muscle tension was estimated from two muscle preparations. The peak value obtained was 103 kN · m^{-2}. The slopes of the regression lines relating temperature to time to peak twitch tension differed significantly between *A. colbecki* and the Southern temperate species *Zygochlamys patagonica* (Fig. 3). The data required to compare *Argopecten irradians* statistically (Olson and Marsh 1993) were not available, but the points for this species were all above the relationship for the other species and fell outside their 95% Confidence Intervals. While these data indicate differences in the intrinsic muscle properties between species more work in a much larger range of species will be required in order to evaluate this further. The overall Q_{10} (0-20^{o}C) of the relationship between temperature and time to peak twitch across all 4 species was 2.05 ($y = 209.12e^{-0.0598x}$).

Discussion

Swimming performances and muscle twitch characteristics in *Adamussium colbecki*, were highly sensitive to temperature changes across their normal *in vivo* temperature range, but showed no evidence for temperature compensation when compared to other species, or any ability to acclimate to temperature changes. Over timescales of hours, weeks or millions of years, temperature would appear to directly control muscle twitch characteristics with

resultant effects on swimming performance (Figures 2 and 3). As similar results have been shown in Antarctic fishes (Johnston and Altringham 1985; Wakeling and Johnston 1998; Hardewig et al. 1999; Wilson et al. 2001), this finding poses general questions about the role and relative importance of swimming and constraints on muscle performance in cold-water animals.

As noted above, the mechanism for the observed trends in whole animal performance appears to be a direct relationship between temperature and the twitch kinetics of the adductor muscle. Little is known about evolution of scallop muscle under different temperature regimes, and whether scallops utilise mechanisms such as altered enzyme isoforms (Johnston et al. 1975) and mitochondrial densities (Johnston et al. 1998) in order to attempt to compensate for thermodynamic and diffusion rate restrictions (as observed in fishes). What is clear is that, whatever mechanisms are used, little evidence for compensation exists in scallops. Antarctic scallops also lacked the ability to acclimate to temperature change within their natural range, and were extremely susceptible to rises above this range. As Peck et al (2004) demonstrated, the ability to swim was soon lost as temperature rose. As in Antarctic fishes, the ability to survive at the stable and low temperatures of Antarctica, was associated with low muscle performance (Wakeling and Johnston 1998), and extreme stenothermy (Wilson et al. 2001).

It is important to consider the ecological context when considering performance measures, and relating performance to features of the habitat to which an animal is adapted. The declines in burst performance with decreasing temperature shown here are from a selection of species that crosses a significant latitudinal range, and therefore might reflect other variables rather than, or in conjunction with, temperature. Several ecological factors probably affect the amount of investment that scallops should optimally devote to muscle performance. The optimum strategy will maximise the average lifetime fecundity of the animals using that strategy, a function of both longevity and annual reproductive investment. Total annual energy supply for herbivores is reduced at high latitudes, and studies in *A. colbecki* indicate

that, despite it's low metabolic rate, this decrease results in a reduction in the energy available for gonadal and somatic development (Heilmayer and Brey 2003). Developing and maintaining a given level of muscle mass and metabolic performance at high latitudes might therefore require a larger proportion of the available energy supply.

This high relative investment will only be adaptive if there is strong selective pressure for high swimming performance in Antarctic scallops. Two potential uses of high performance swimming are to allow the animal to break free of and out-accelerate predators, and to generate sufficient downwards thrust and lift to support the mass of the animal. Our field studies showed that the Rothera *A. colbecki* population suffered minimal predation, and would probably be unable to escape immediately if attacked, as the animals were attached to rocks by byssal threads. The absence of crabs in the high Antarctic (Thatje and Arntz 2004) means that the type of predation on *A. colbecki* is altered, shifting the balance towards slow-moving molluscs and seastars. The observed predator-pressure on *A. colbecki* is much lower than has been demonstrated in some temperate environments (Bologna and Heck 1999), where crabs often exerted a high proportion of this pressure (Hatcher et al. 1996; Barbeau et al. 1998). The absence of crabs is due to the inability of decapods to maintain activity at such low temperatures (Frederich et al. 2001), and is therefore probably an indirect (ecologically mediated) effect of temperature on scallop swimming. Loss of crushing predators such as crabs may have a further effect on scallop swimming, by reducing the selective pressure for shell thickness and density. Our data showed that *A. colbecki* was able to swim at velocities that would not be sufficient to support the mass of more heavily shelled species such as *Aequipecten opercularis* (Thorburn and Gruffydd 1979). Reduced shell mass in the Antarctic scallop may allow swimming without high muscle performances, and may also explain why muscle tension in *A. colbecki* was only half that recorded in *Argopecten irradians* (Olson and Marsh 1993) as the weak shell of the Antarctic species might not be capable of withstanding higher forces. Whether any systematic trends in predator pressure on scallops occur with changes in temperature and latitude remains uncertain, though this has been suggested in

Argopecten irradians (Wilbur and Gaffney 1997). At one end of the temperature spectrum ecological factors certainly appear to interact with physiological effects to define the performance envelope.

Conclusions

The swimming and muscle performances of *A. colbecki* showed no evidence of compensation, or ability to acclimate to temperature change. As *A. colbecki* is a very common species throughout Antarctic waters, this level of investment in its locomotory system must be a successful strategy. A combination of thermodynamic constraints, low overall energy availability, and reduced selective pressure for swimming ability and shell strength, probably explain the low levels of swimming performance seen in *Adamussium colbecki*.

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Figure Legends

Fig. 1 Clap duration against temperature during the first clap of escape swimming in the Antarctic scallop, *Adamussium colbecki*. Pooled data for animals acclimated to –1, 0 or 2oC and swimming within 2^{o}C of their acclimation temperature. Data presented are means ± 1SE. Clap duration was significantly negatively related to temperature (r^2 = 0.45, p < 0.001, df = 42, y = -0.048 x +0.578).

Fig. 2 Comparison of the whole-body performance of *Adamussium colbecki* (solid circles) to that of other species. Mean velocity (± 1 S.E.) is plotted against temperature with data for *Aequipecten opercularis* (Bailey 2001) (open circles), *Placopecten magellanicus* #1, (Manuel and Dadswell 1990) and #2, (Cheng et al. 1996) (solid and open triangles respectively) and *Amussium pleuronectes* (Morton 1980) (solid squares). Data for all species were fitted to a single exponential function ($y = 0.1017e^{0.0727x}$) giving a Q10 (1-20^{o}C) of 2.08. All animals were of similar shell height (63-67 mm) except for *P. magellanicus* #1 (4-35 mm).

Fig. 3 Time to peak twitch force during isometric contractions. Data are presented (means ± 1 S.E.) for *Adamussium colbecki* (solid circles), *Aequipecten opercularis* (open circles), *Zygochlamys patagonica* (solid triangles) (Bailey 2001), and *Argopecten irradians* (open triangles) (Olson and Marsh, 1993). Time to peak twitch fell with increasing temperature in all species. The slopes of the relationship between temperature and time to peak twitch differed between *A. colbecki* and *Z. patagonica* (t-test, p = 0.05, df = 16).

Figures

Fig. 1

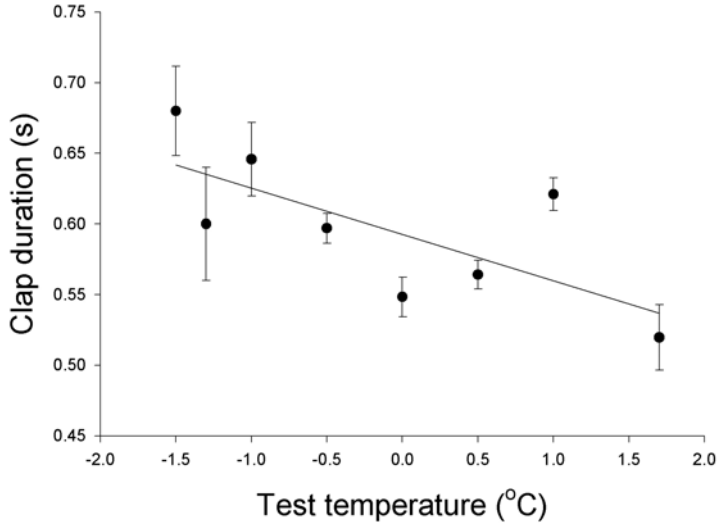


Fig. 2

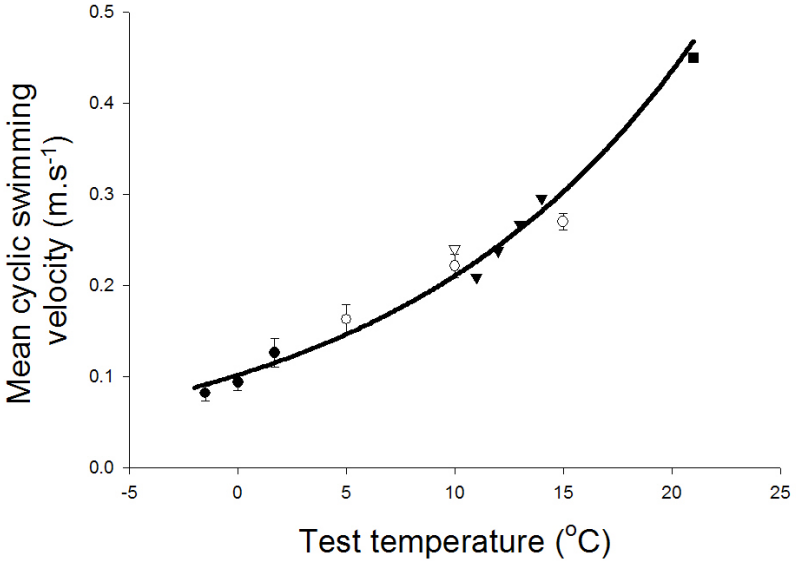
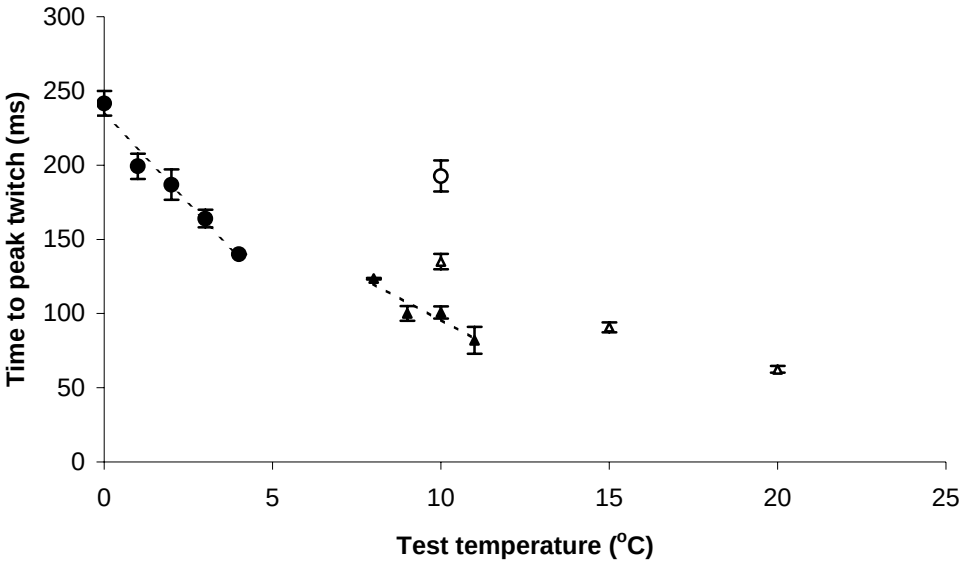


Fig. 3


Time to peak twitch (ms)
300
250
200
150
100
50
0
0
5
10
15
20
25
Test temperature (°C)