

# Jet propulsion in the cold: mechanics of swimming in the Antarctic scallop *Adamussium colbecki*

Mark Denny\* and Luke Miller

Hopkins Marine Station of Stanford University, Pacific Grove, CA 93950, USA

\*Author for correspondence (e-mail: mwdenny@stanford.edu)

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## Summary

Unlike most bivalves, scallops are able to swim, relying on a shell with reduced mass and streamlined proportions, a large fast-twitch adductor muscle and the elastic characteristics of the shell's hinge. Despite these adaptations, swimming in scallops is never far from failure, and it is surprising to find a swimming scallop in Antarctica, where low temperature increases the viscosity of seawater, decreases the power output of the adductor muscle and potentially compromises the energy storage capability of the hinge material (abductin, a protein rubber). How does the Antarctic scallop, *Adamussium colbecki*, cope with the cold? Its shell mass is substantially reduced relative to that of temperate and tropical scallops, but this potential advantage is more than offset by a

drastic reduction in adductor-muscle mass. By contrast, *A. colbecki*'s abductin maintains a higher resilience at low temperatures than does the abductin of a temperate scallop. This resilience may help to compensate for reduced muscle mass, assisting the Antarctic scallop to maintain its marginal swimming ability. However, theory suggests that this assistance should be slight, so the adaptive value of increased resilience remains open to question. The high resilience of *A. colbecki* abductin at low temperatures may be of interest to materials engineers.

Key words: abductin, *Adamussium colbecki*, Antarctic, jet propulsion, scallop, swimming.

## Introduction

Of the 17 000 known species of bivalve molluscs, only a few – most notably the scallops and file shells – are capable of swimming (e.g. Gould, 1971; Donovan et al., 2004). By rapidly clapping their valves together, these unusual clams expel jets of water from the dorsal edge of the shell. The resulting thrust propels the animals ventrally (Gould, 1971; Cheng and DeMont, 1996), allowing them to escape from both predators and environmental stress, and potentially allowing them to migrate (Morton, 1980).

As with all jet-propelled animals, swimming in scallops and file shells depends on the ability to rapidly expel fluid (thereby producing thrust) and then to re-inflate. The more frequently the animal can perform this cycle, the more thrust is produced in a given time and the more power is available to propel the body. The consequences of increased power of thrust are potentially valuable: the larger the power, the larger the mass that can be lifted against gravity, and the faster the animal moves.

Pertinent characteristics of this system emerge if, in a heuristic model, we treat the jet-inflation cycle as the oscillation of a spring-mass system (Fig. 1). The mass,  $m$ , of the moving parts of the system is a combination of the mass of the shell and the 'added mass' of water that acts as if it moves with the

shell (Batchelor, 1967). During a jet (Fig. 1A), the adductor muscle acts as a spring, applying a force to clap the valves together. The rotational stiffness of this spring (the proportionality between force and angular deflection) is  $K_m$ . During inflation (Fig. 1B), a pad of rubbery material in the shell's hinge (the resilium) acts as a spring, applying a force to spread the valves apart. The rotational stiffness of the resilium is  $K_r$ . As the shell moves (during both jetting and inflation), energy is lost to viscous process. The effect of these losses is quantified by the damping coefficient,  $\zeta$ , which varies between 0 (no damping) and 1 (critical damping, for which oscillation is minimized). Given these assumptions, we can predict the time required for either a jet,  $t_{\text{jet}}$ , or inflation,  $t_{\text{inf}}$  (Thomson, 1986):

$$t_{\text{jet}} = \frac{1}{2} \sqrt{\frac{m}{K_m(1-\zeta^2)}}, \quad (1)$$

$$t_{\text{inf}} = \frac{1}{2} \sqrt{\frac{m}{K_r(1-\zeta^2)}}. \quad (2)$$

The overall time needed for a jet–inflation cycle is the sum of these two times, and the frequency of the cycle – which is

proportional to the power available for thrust – is the inverse of the overall cycle time:

$$\text{power} \propto \text{frequency} = \frac{1}{t_{\text{jet}} + t_{\text{inf}}} = \frac{2\sqrt{1-\zeta^2}}{\sqrt{\frac{m}{K_m}} + \sqrt{\frac{m}{K_r}}} \quad (3)$$

Thus, the thrust power available to a jet-propelled bivalve increases if the mass or the damping coefficient is decreased or the stiffness of the springs is increased. From this simple heuristic model, we predict that if increased thrust has been a factor in the mechanical evolution of scallops,  $K_m$  and  $K_r$  should be relatively large and  $m$  and  $\zeta$  should be relatively small compared with sedentary clams.

These expectations are borne out in nature. The adductor muscle of a scallop (the muscle responsible for clapping the valves together) forms an unusually large proportion of the overall mass of the animal (typically ~25%) and has striated fibers that contract rapidly relative to the muscles found in other bivalves (Rall, 1981; Marsh et al., 1992; Marsh and Olson, 1994). Both factors increase  $K_m$ , the apparent stiffness of the system's spring during a jet, and thereby increase the power of thrust (Eqn 3). The shell mass in swimming bivalves is reduced relative to their sedentary cousins, which both increases the power of thrust (Eqn 3) and simultaneously reduces the need for thrust by reducing the weight that must be lifted against gravity (Gould, 1971). Lastly, the resilium is formed from a stiff elastic material – abductin – that causes the shell to open rapidly after it has clapped shut (Gould, 1971; Cheng and DeMont, 1996), and the mechanical resilience of abductin (its ability to store the potential energy of deformation with little loss to viscous processes) reduces the damping of the system.

Although these adaptations allow scallops to swim, these bivalves are nonetheless on the verge of failure. If scallops' shells were slightly bigger, if their muscles were capable of producing slightly less power, or if their abductin were less resilient, these animals might never get off the seafloor. For example, during ontogeny, the weight of scallops increases faster than their ability to produce thrust, and, as a consequence, adults above a certain size are inefficient

swimmers and may be incapable of swimming altogether (Gould, 1971; Dadswell and Weihs, 1990; Cheng and DeMont, 1996).

The ability of scallops to swim is put to a stringent test by the Antarctic scallop, *Adamussium colbecki*. In this animal's frigid habitat ( $-1.8^\circ\text{C}$ ), water is approximately 43% more viscous than at  $10^\circ\text{C}$ , where most temperate scallops live. Increased viscosity amplifies the power required both to form a propulsive jet and to push the animal through the water. At the same time, low temperature has the potential to decrease the power output of the adductor muscle. Furthermore, the resilience of rubbery materials (such as abductin) typically decreases at low temperatures. For example, the decrease in resilience of a rubber O-ring contributed to the loss of the space shuttle *Challenger* when the craft was launched at temperatures near freezing. A decrease in the resilience of its abductin pad would increase the damping coefficient of the Antarctic scallop's spring-mass system, potentially reducing the power available for thrust (Eqn 3).

Despite these potential problems, *A. colbecki* is capable of swimming. However, it is evident that the Antarctic scallop is on the edge: *A. colbecki* swims at speeds of only 25–50% of those found in temperate scallops (Ansell et al., 1998), barely above the minimal speed required to stay aloft (Cheng and DeMont, 1996).

In this study, we address the question of what physiological and mechanical strategies allow *A. colbecki* to maintain its swimming ability in such an extreme environment. In light of our heuristic model, there are five likely possibilities, listed here in decreasing order of apparent effectiveness and practicality.

(1) For an animal of a given size, its mass could decrease. This adaptation would be most effectively accomplished by decreasing the mass of the high-density shell, which would both increase the frequency of clapping and decrease the need for thrust.

(2) The rotational stiffness during inflation,  $K_r$ , could be maintained or increased by adjusting the size of the resilium or the stiffness of its abductin.

(3) Power output could be maintained by maintaining the 'stiffness',  $K_m$ , of the adductor muscle, in essence by maintaining the force and speed with which the muscle contracts. There are problems with this strategy. First, prior research has shown that *A. colbecki*'s muscle physiology has not compensated for low temperature. The time to peak twitch force is longer and maximum muscle tension is lower for *A. colbecki* adductor muscle than for the muscle of temperate scallops (Bailey et al., 2005), suggesting that the mass-specific power output of *A. colbecki* is reduced relative to its temperate cousins. As a consequence, to maintain  $K_m$ , *A. colbecki* would have to increase the mass of the adductor muscle relative to that of the shell and body. This increase would raise a second problem: extra metabolic energy would be needed to maintain the increased mass of this active muscle.

(4) The damping coefficient for the system,  $\zeta$ , could be reduced by reducing viscous losses within the abductin pad.

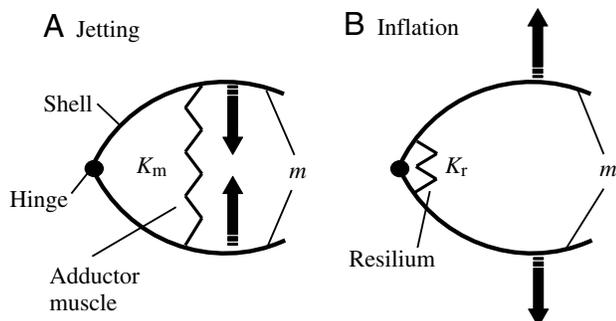


Fig. 1. A heuristic model for the jet-inflation cycle in a swimming scallop (see text). See Table 1 for a definition of symbols.

Again, there is a potential problem. As noted above,  $\xi$  is in part determined by the resilience of abductin, but  $\xi$  also depends on hydrodynamic damping as the valves move through the water. Of these two, hydrodynamic damping is much the larger. As a result, even large changes in the resilience of abductin are likely to produce only small changes in the overall damping coefficient, and hence in the power available for thrust.

(5) As a spring-mass system, *A. colbecki* could use the resilience of its abductin pad to act as a resonant mechanical oscillator during swimming (DeMont, 1990). It is unclear, however, how effective this strategy could be. On one hand, by clapping the valves at their resonant frequency, *A. colbecki* could minimize the energy expended by the adductor muscle to overcome the inertia of the shell. On the other hand, the metabolic savings are likely to be small. Only a minor fraction of the total energy expenditure is used to overcome the inertia of the shell, and Alexander suggests that for scallops in general “any energy-saving effect of the abductin is trivial” (Alexander, 2003).

In summary, there are a variety of strategies for scallops to cope with the cold. *A priori*, one would suspect that decreasing shell mass and maintaining the stiffness of the resilium would be the least problematic, and adjustment of the resilience of abductin would be the least effective.

As a first step toward evaluating jet propulsion in *A. colbecki*, we address seven questions related to the potential adaptive strategies listed above.

(1) Is the shell mass of Antarctic scallops reduced relative to that of temperate and tropical scallops?

Have (2) the adductor muscle mass, (3) rotational stiffness of the shell-hinge system and (4) stiffness of abductin increased in *A. colbecki* relative to temperate and tropical scallops?

(5) Does *A. colbecki* clap at its resonant frequency?

(6) Is the abductin of the Antarctic scallop indeed an entropy elastomer and therefore subject to decreased resilience at low temperature?

(7) If so, has abductin in *A. colbecki* adjusted to maintain high resilience in the cold?

### Materials and methods

Adult *Adamussium colbecki* (Smith 1902) were collected by divers in November 2005 at New Harbor, McMurdo Sound, Antarctica and maintained in a flow-through aquarium at  $-1.8^{\circ}\text{C}$  at McMurdo Station on Ross Island. Experiments were conducted in January 2006, at which time the animals were healthy and capable of active swimming.

#### Morphometry

Body dimensions and masses were noted for 15 animals. Shell dimensions were measured to the nearest 0.05 mm using Vernier calipers. The soft body parts were separated from the shell, and the adductor muscle and remainder of the soft tissues were blotted and weighed separately to the nearest 0.01 g.

#### Shell density

The density of four *A. colbecki* shells was determined by weighing each shell in air (to the nearest mg) and then weighing the same shell when suspended by a thin thread in distilled water.

#### Weight in water

The weight in water of the soft tissue and shell of *A. colbecki* were calculated using the measured density of the shell, a density of  $1027\text{ kg m}^{-3}$  for seawater (salinity=33‰,  $-1.8^{\circ}\text{C}$ ), and an assumed density of  $1080\text{ kg m}^{-3}$  for soft tissue (Denny, 1993).

#### Resonant frequency

Clapping frequency during active swimming was measured for two individuals in the Station holding tanks. Scallops were induced to swim by squirting them with freshwater, and the resulting bouts of swimming were recorded with a video camera. Clapping frequency =  $1/\text{mean time between claps}$ .

For comparison, the resonant frequency of the shell-resilium system was determined for two specimens of *A. colbecki* (Fig. 2). The body was dissected from the shell, leaving the hinge and resilium intact, and the lower valve of the shell was glued to a massive weight. The shell was then submerged in a large (approximately  $0.6\text{ m}^2 \times 6.0\text{ m} \times 0.2\text{ m}$  deep) vat of

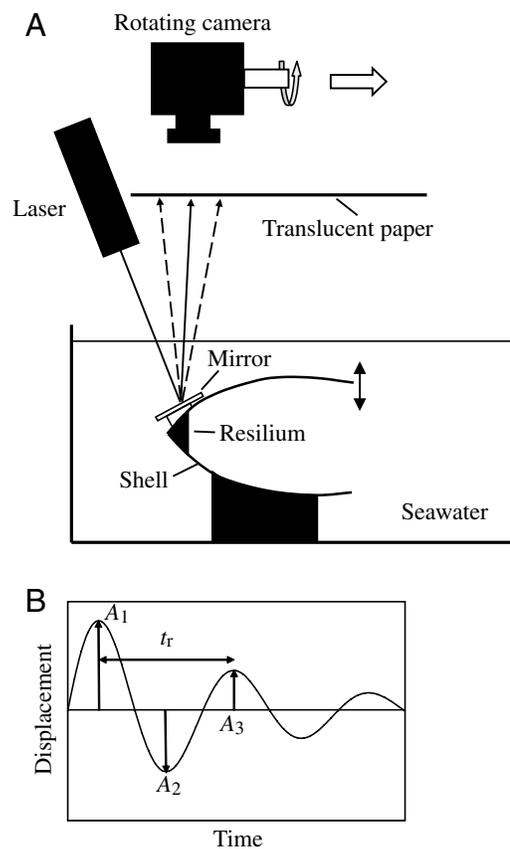


Fig. 2. The apparatus used to measure the resonant frequency and logarithmic decrement of the shell-hinge system. See Table 1 for a definition of symbols.

seawater (at 8°C), and a small mirror was glued over the hinge on the upper valve. A laser beam reflecting from this mirror onto translucent paper held horizontal over the vat allowed us to measure the angle of the upper valve, which was depressed until it met the lower valve and was then released. The subsequent damped oscillation of the upper valve was recorded by a rotating camera set for a long exposure. The system was less than critically damped, but only the first three half-cycle amplitudes were large enough to be accurately measured. Examination of this image allowed us to measure the resonant period with which the shell oscillated. Resonant frequency = 1/resonant period.

Because only one shell moves, the resonant frequency measured in this experiment is less than that expected of a free-swimming scallop. According to the model of DeMont (DeMont, 1990), the free-swimming resonant frequency is  $\sqrt{2}$  times the experimentally measured frequency.

#### Damping coefficient and system resilience

The record of shell angle through time also allowed us to measure the amplitude of shell deflection,  $A_i$ , for consecutive half cycles of deflection ( $i=1, 2, 3, \dots$ ; see Fig. 2), from which the damping coefficient of the shell-resilium system can be determined as follows. The slope,  $B$ , of a plot of the natural logarithm of  $A_i$  versus half-cycle number ( $i$ ) allows us to specify the logarithmic decrement,  $\delta$  (Alexander, 1966):

$$\delta = -B. \quad (4)$$

The logarithmic decrement of oscillation can in turn be related to the damping coefficient (Appendix):

$$\zeta = \frac{1}{\sqrt{\frac{\pi^2}{\delta^2} + 1}}. \quad (5)$$

Here, we are concerned with all viscous losses as the intact shell opens and closes, a combination of losses due both to viscous effects within the resilium and to interaction of the shell with water around it. As the damping coefficient of the whole shell increases, the damped period of oscillation also increases, the power available for thrust decreases (Eqn 3) and at some point the animal may no longer be able to swim.

The logarithmic decrement can also be used to calculate the resilience,  $R_s$ , of the shell-resilium system (Alexander, 1966):

$$R_s = \exp(-2\delta). \quad (6)$$

If there is no viscous loss of energy,  $R_s=1$ . If 90% of the energy initially imparted to the system is retained in each half cycle,  $R_s=0.9$ , and so forth. Note that the logarithmic decrement used here ( $\delta$ , based on the decrease in amplitude from one half cycle to the next) is half the value often used in the engineering literature ( $\delta_e$ , based on the decrease in amplitude per full cycle).

Note that the damping coefficient of the shell-hinge system can be calculated in terms of the system's resilience. Solving Eqn 6 for  $\delta$  and inserting the result into Eqn 5, we see that:

$$\zeta = \frac{1}{\sqrt{\frac{4\pi^2}{(\ln R_s)^2} + 1}}. \quad (7)$$

Due to the large angular change in shell orientation and refraction of the light beam by the water's surface, measurements of the logarithmic decrement could not be easily obtained from experiments in which the shell moved through its entire range of gape. A second set of experiments was conducted in which the shell was induced to oscillate through a small angle, and these experiments were used to estimate the logarithmic decrement of the shell-hinge system.

#### Thermoelastic measurements

Determination of the elastic mechanism of *A. colbecki* abductin followed the reasoning of Alexander (Alexander, 1966) and Shadwick and Gosline (Shadwick and Gosline, 1985). In any elastic material, the force,  $F$ , required to resist an imposed change in length,  $L$ , at constant absolute temperature,  $T$ , and volume,  $V$ , is due to changes in the material's internal energy,  $U$ , and its entropy,  $S$  (a measure of the material's disorder):

$$F = \frac{\partial U}{\partial L_{T,V}} - T \frac{\partial S}{\partial L_{T,V}}. \quad (8)$$

Deformation of an ideal rubber involves rearrangement of the constituent polymer chains, but negligible stretching or compression of bonds within the chains, so the change in internal energy ( $\partial U/\partial L_{T,V}$ ) accounts for little of the force of deformation. Instead, the force required to deform a rubber is primarily due to changes in entropy as chains are rearranged ( $\partial S/\partial L_{T,V}$ ). Either compression or extension of a rubber network imposes order on the otherwise randomly arranged chains, and this decrease in entropy results in an increased force.

The nature of the resistive force in a material can be determined by measuring the relative contributions of internal energy and entropy. As a practical matter, changes in these parameters are not measured directly. Instead, we utilize aspects of the theory of rubber elasticity to formulate a feasible measurement strategy (Flory, 1953; Treloar, 1975; Shadwick and Gosline, 1985).

First, we note that it is very difficult to measure changes in entropy at constant volume for biological elastomers in an aqueous environment. As the material is stretched or compressed, water tends to enter or leave, and volume changes. However, the change in entropy with change in length in an elastomer is approximately equal in magnitude (but opposite in sign) to change in force with change in temperature, provided the swelling of the material is allowed to come to equilibrium:

$$-\frac{\partial S}{\partial L_{T,V}} \approx \frac{\partial F}{\partial T_{\lambda, P, eq}}. \quad (9)$$

Note that the derivative of entropy with respect to length is taken at constant temperature and volume, whereas the derivative of force with respect to temperature is taken while maintaining the material at constant pressure,  $P$ , and constant compression ratio,  $\lambda$ . Compression ratio is the ratio of undeformed length to deformed length. Thus, the theory of rubber elasticity predicts that the force involved in deforming a material (Shadwick and Gosline, 1985) is:

$$F \approx \frac{\partial S}{\partial L_{T,V,\text{eq}}} + T \frac{\partial F}{\partial T_{\lambda,P,\text{eq}}} . \quad (10)$$

This equation is a recipe for a standard thermoelastic experiment. A sample is deformed to a given compression ratio, and the force required to maintain this ratio is measured as a function of temperature. Temperature is changed slowly to allow the material to maintain swelling equilibrium. The entropic contribution to force is the slope of the line of force *versus* temperature, and the internal energy contribution,  $\partial U/\partial L_{T,V,\text{eq}}$ , is the calculated force at 0 K. For an ideal entropy elastomer,  $\partial U/\partial L_{T,V,\text{eq}} \approx 0$  and all the force is due to  $T(\partial F/\partial T_{\lambda,P,\text{eq}})$ .

To make use of Eqn 10, thermoelastic experiments were conducted on four *A. colbecki* specimens, as shown in Fig. 3. The body of the scallop was removed, leaving only the shell and resilium. The shell was held rigidly suspended in a seawater bath, and a string (#2 nylon suture) was attached to the lower valve. The string passed upwards through a slot cut into the upper valve and was attached to one end of a balanced beam. The core of a linearly variable differential transformer (LVDT, Schaevitz 500HR; Schaevitz Engineering, Camden, NJ, USA) was suspended from the other arm of the beam and in turn supported a pan onto which weights could be placed. In this fashion, force could be applied to compress the resilium, and the resulting deflection of the lower valve was measured by the LVDT. Voltage output from the LVDT was fed to a chart recorder (Omniscrite; Houston Instruments, Houston, TX,

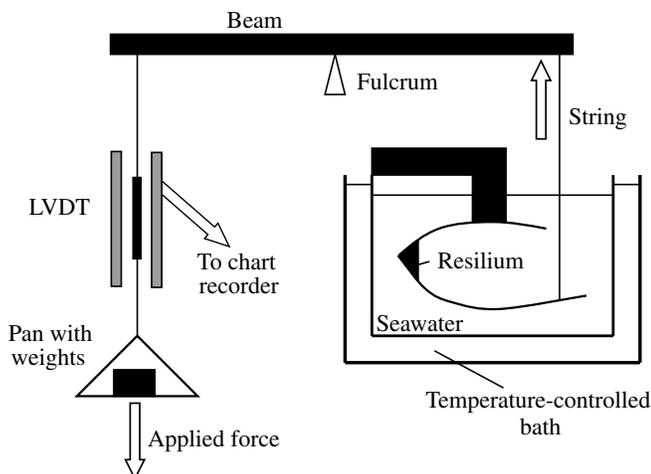


Fig. 3. The apparatus used to measure the thermoelastic properties of abductin.

USA), and the apparatus was calibrated so that the proportionality between deflection of the valve and deflection of the chart-recorder pen was accurately known. The weight of the LVDT core and pan was counteracted by adding Plasticine™ to the opposite arm of the beam, leaving just sufficient tension to pull the thread taut in its attachment to the lower valve. The seawater bath enclosing the shell sat in a controlled temperature bath, allowing experiments to be conducted at a range of temperatures (0, 10, 20 and 30°C). At each temperature, a series of weights was added to the pan, and the resulting deformations were recorded. The sample crept slightly upon application of force, and to standardize this effect, deformations were measured at a uniform time (16 s) after each force was applied. The sample was allowed to fully recover its initial length after each imposition of an applied force.

The abductin sample swelled with increasing temperature, and sufficient time was allowed for swelling to come to equilibrium before tests were conducted. The gape of the shell was measured to the nearest 0.05 mm at 20°C, and this was taken as the reference length when calculating compression ratios. Change in unloaded length as a function of temperature was measured as an integral part of the experiment, allowing the force–deformation curve for each temperature to be converted to a curve of force *versus* compression ratio.

Applied force was normalized to the size of each resilium by converting force to stress ( $\sigma$ , force per cross-sectional area of abductin) through a consideration of the geometry of the shell and resilium and the application of basic materials mechanics (Fig. 4). First, we note that:

$$\sigma \equiv \frac{E}{\lambda - 1} , \quad (11)$$

where  $E$  is the stiffness of the material (its elastic modulus).

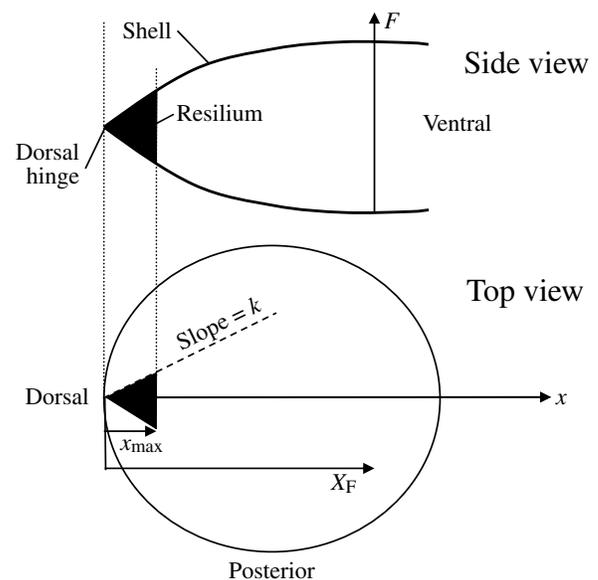


Fig. 4. The geometry of the shell used to calculate stress in the resilium.

Next, we note that  $M_F$ , the moment applied by the external force, is equal to the product of applied force,  $F$ , and the lever arm,  $X_F$ .

$$M_F = F X_F . \quad (12)$$

When stressed, the resilium compresses until the resisting moment it applies to the shell,  $M_R$ , is equal to, and opposite,  $M_F$ .  $M_R$  is in turn calculated as follows. The resilium is approximately triangular in both anterior–posterior and dorsal–ventral cross section. With  $x$  measured from the dorsal tip of the resilium (at the shell's hinge), a small element of cross-sectional area,  $da=2kx dx$ , where  $k$  is the slope of a side of the triangle (see Fig. 4). Because left–right thickness of the resilium increases in proportion to  $x$ , rotation of the lower valve imposes the same compression ratio on all portions of the resilium. Thus, if the stiffness of resilium material ( $E$ ) is everywhere the same, the stress imposed on the resilium is everywhere the same (Eqn 11), and the force generated by the compression of this small bit of area is:

$$dF_R = 2\sigma kx dx . \quad (13)$$

The infinitesimal moment produced by this force is the product of force (Eqn 13) and its moment arm,  $x$ :

$$dM_R = xdF_R = 2\sigma kx^2 dx . \quad (14)$$

The overall moment generated by the resilium is the integral of this infinitesimal moment taken across the full length of the resilium,  $x_{\max}$ :

$$M_R = 2\sigma k \int_0^{x_{\max}} x^2 dx = \frac{2\sigma kx_{\max}^3}{3} . \quad (15)$$

Setting Eqn 12 equal to Eqn 15 and solving for stress, we find that:

$$\sigma = \frac{3X_F F}{2kx_{\max}^3} . \quad (16)$$

Thus, stress in the resilium can be calculated from the known applied force and the dimensions of the sample.

In summary, by applying weight to the pan and measuring the resulting deflections of the lower valve, a  $\sigma$ – $\lambda$  curve was obtained for each experimental temperature.

From these  $\sigma$ – $\lambda$  relationships, stress *versus* temperature curves were drawn for each of five constant compression ratios, and a linear regression was fit to each curve. For each curve, the slope of the line and y intercept (and their 95% confidence limits) were then calculated using standard statistics, thereby providing information about the entropy and internal energy contributions to the total stress at each compression ratio (Eqn 10).

#### Rotational stiffness

The apparatus used for the thermoelastic experiments (Fig. 3) also allowed us to measure the rotational stiffness of the resilium for the four test shells. As noted above, imposition of an applied moment,  $M_F$ , resulted in a measured displacement

of the lower valve. Dividing this displacement by the moment arm,  $X_F$  (see Fig. 4), provides a close approximation of the angular displacement of the valve.  $M_F$  divided by this angular displacement is the rotational stiffness ( $\text{Nm rad}^{-1}$ ).

#### Abductin resilience

The resilience,  $R_a$ , of *A. colbecki* abductin (as distinct from  $R_s$ , the resilience of the shell-resilium system) was measured in a manner similar to that used by Alexander (Alexander, 1966). The body was removed from a shell, leaving the resilium intact, and the lower valve was glued firmly to a weight and placed in a beaker. Seawater (salinity=33‰) was added to the level of the resilium and the beaker was then placed in a constant-temperature bath (Fig. 5). To reduce viscous losses from the interaction of the shell and air, the upper valve was trimmed until only a small area surrounding the hinge was left. A light, rigid plastic beam was then glued to the upper valve, and Plasticine™ was added to the free end of this beam to adjust the resonant frequency of the sample to 3–4 Hz, the same frequency used for tests on temperate scallops (Alexander, 1966; Bowie et al., 1993). A small mirror was then mounted (using Plasticine™) over the hinge of the shell. The beam from a laser pointer reflected from this mirror and shone on the ceiling, providing a measure of the shell's angle. When the plastic beam was momentarily deflected and then released, the shell oscillated resonantly, and the amplitude of the oscillations (measured from the location of the image of the laser beam on the ceiling) was recorded by a rotating camera set for a 2.5 s exposure. This image allowed us to measure the amplitude of

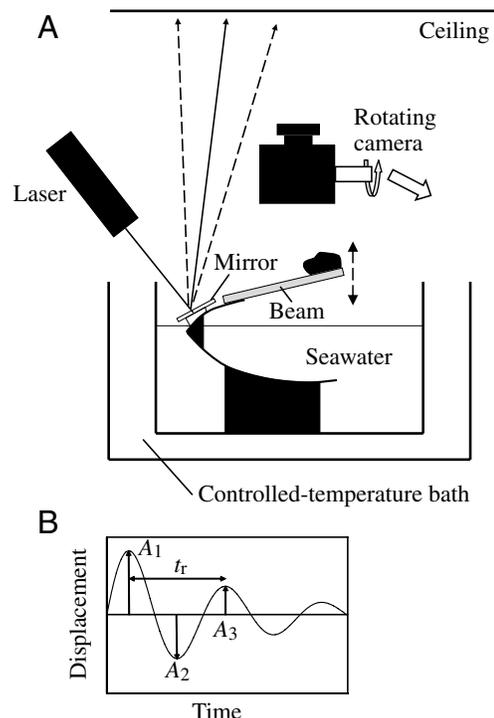


Fig. 5. The apparatus used to measure the resilience of abductin. See Table 1 for a definition of symbols.

shell deflection,  $A_i$ , for consecutive half cycles of deflection ( $i=1, 2, 3\dots$ ), from which the logarithmic decrement and resilience were calculated as for the overall system (Eqns 4, 6).

Resilience in *A. colbecki* abductin was compared to that in a temperate species (*Placopecten magellanicus*). Data were extracted from fig. 2 of Bowie et al. (Bowie et al., 1993) for temperatures used in this study (0, 5, 10, 15, 20, 30,  $\pm 1^\circ\text{C}$ ) and were compared to our data using a two-factor analysis of variance with temperature and species as the two fixed factors (SysStat 11.0; SPSS Inc., Chicago, IL, USA). Planned comparisons were then used to test for a difference in mean resilience at each temperature.

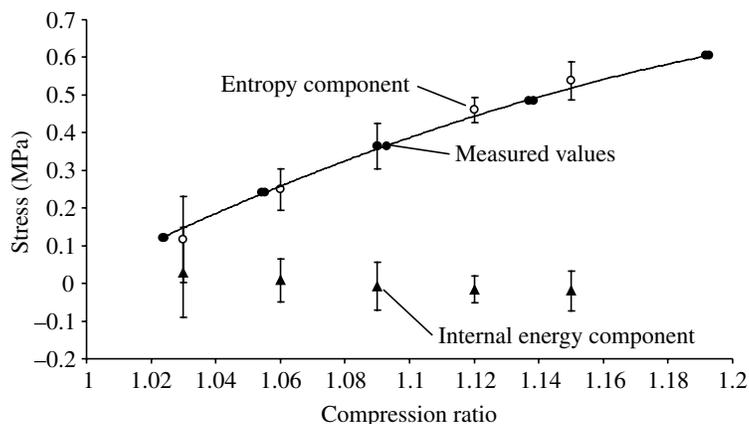
#### Amino acid composition

Amino acid composition was determined for abductin from two species of scallops: *A. colbecki* (collected in McMurdo Sound) and *Pecten maximus* L. (collected at Tjarnö Marine Biological Station on the west coast of Sweden). The resilium was dissected from three individuals of each species. Half of each sample was soaked in formic acid at  $4^\circ\text{C}$  overnight and then hydrolyzed in  $6\text{ mol l}^{-1}$  HCl/1% phenol at  $110^\circ\text{C}$  for 24 h. The second half of each sample was soaked in performic acid overnight to oxidize cysteine, cystine and methionine prior to hydrolysis. All samples were then analyzed on a Hitachi L-8800 analyzer with a sodium citrate buffer system. Analyses were performed by the Molecular Structure Facility at the University of California, Davis. Similarity among scallop species was quantified using the Bray-Curtis similarity coefficient (Primer; Primer-E Ltd, Plymouth, UK).

## Results

### Body dimensions and masses

The mean dorsal–ventral length of *A. colbecki* shells in our sample was  $86.4\pm 6.4$  mm (s.d.,  $N=15$ ). The shell material of *A. colbecki* has a density of  $2644\pm 22$   $\text{kg m}^{-3}$  ( $N=4$ ). The ratio of shell mass to wet body mass (adductor muscle plus other soft tissue) was  $0.59\pm 0.12$  ( $N=15$ ), and the ratio of adductor muscle mass to the total mass of soft tissue was  $0.26\pm 0.049$  ( $N=15$ ).



### Resonant oscillation

Resonant frequencies of oscillation in the two experimental shells were 1.42 Hz (for a shell with a dorsal–ventral length of 79.6 mm) and 1.02 Hz (for a shell with dorsal–ventral length of 88.4 mm). These correspond to free-swimming resonant frequencies of 2.00 and 1.45 Hz, respectively. These free-swimming resonant frequencies are approximately equal to the clapping frequencies measured both in the holding tanks (1.39 and 1.46 Hz) and in the field [1.32–2.08 Hz, mean=1.52 Hz (Ansell et al., 1998)].

### Damping coefficient and system resilience

The mean logarithmic decrement for the whole-shell system was  $0.69\pm 0.08$  (s.d.,  $N=6$ ), corresponding to a damping coefficient of  $\xi=0.215\pm 0.02$  ( $N=6$ ; Eqn 5) and a resilience  $R_s=0.252$  (Eqn 6).

### Thermoelastic experiments

The results of a representative experiment are shown in Fig. 6. The internal energy contribution to stress is statistically indistinguishable from 0, and the entropy contribution is statistically indistinguishable from the measured stress, indicating that *A. colbecki* abductin is an entropy rubber.

Representative stress–compression ratio curves are shown in Fig. 7. Stiffness decreases slightly with increasing compression ratio. At  $1.1^\circ\text{C}$ , the tangent elastic modulus (the slope of the curve) varies from 4.0 MPa at low compression ratios to 1.7 MPa at high compression ratios. At  $29.3^\circ\text{C}$ , the material is stiffer, with modulus values that range from 4.6 MPa to 2.3 MPa.

Length of abductin increases by  $0.14\pm 0.07\%$   $\text{deg}^{-1}$  (s.d.,  $N=4$ ). If we assume that abductin swells isometrically, this suggests that volume increases  $0.41\pm 0.20\%$   $\text{deg}^{-1}$  ( $N=4$ ).

### Rotational stiffness

At  $0.4$ – $1.1^\circ\text{C}$ , the mean rotational stiffness of the four test shells was  $0.034\pm 0.019$   $\text{Nm rad}^{-1}$ .

### Resilience

Resilience of *A. colbecki* abductin is variable among samples and decreases with decreasing temperature (Fig. 8). The decrease in resilience for the Antarctic species is less pronounced than that for the temperate species: at low temperatures (0, 5 and  $10^\circ\text{C}$ ), the resilience of *A. colbecki* is significantly higher than that of its temperate relative (Tables 2, 3). For a given temperature, the Antarctic scallop is approximately 3% more resilient. For a given resilience, *A. colbecki* performs as if it were approximately  $5^\circ\text{C}$  warmer.

Fig. 6. Results of a representative thermoelastic experiment. The component of force due to internal energy is negligible, while that due to entropy closely approximates the total force, indicating that *A. colbecki* abductin is an entropy elastomer.

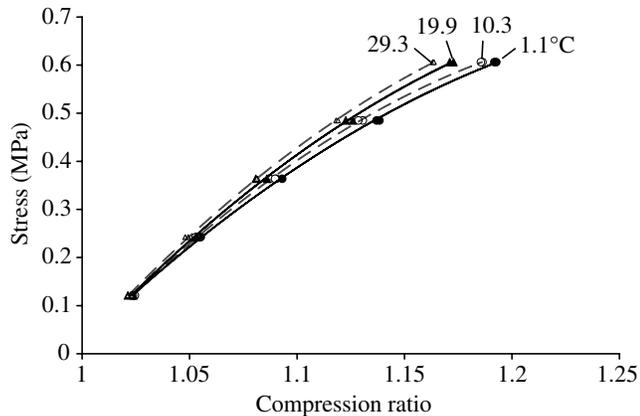


Fig. 7. Stress-compression ratio curves for *A. colbecki* abductin at four temperatures.

#### Amino acid composition

The amino acid composition of *A. colbecki* abductin is given in Table 4, and its similarity to other scallops is shown in Table 5.

#### Discussion

The density of *A. colbecki* shell ( $2644 \text{ kg m}^{-3}$ ) is similar to that of other mollusk shells [ $2700 \text{ kg m}^{-3}$  (Gould, 1971; Wainwright et al., 1974)] and indicates that (as with temperate scallops) the shell is composed primarily of calcite (density =  $2720 \text{ kg m}^{-3}$ ) rather than aragonite [density =  $2930 \text{ kg m}^{-3}$  (Vermeij, 1993)]. Thus, any reduction in *A. colbecki* shell mass has not been accomplished by a substantial reduction in shell density.

By contrast, the morphology, muscle performance and materials mechanics of the Antarctic scallop differ substantially from those of temperate scallops. To place our morphological data in context, we compare values for *A. colbecki* of length equal to the average of our sample to values for a tropical scallop (*Amusium pleuronectes*) with the same length [calculated from data given by Morton (Morton, 1980)].

#### Shell mass

In the Antarctic scallop, the ratio of shell mass to wet body mass (adductor muscle plus other soft tissue) was 0.59, considerably smaller than the ratio in the tropical scallop, 1.07. As a consequence, for our sample, the weight of an average *A. colbecki* in seawater is 61 mN, whereas the weight in water of a similar size tropical scallop is 110 mN. For a given size animal, the Antarctic scallop need provide less thrust to propel its body up from the substratum.

#### Muscle mass

However, the mass of the adductor muscle is also reduced. The ratio of adductor muscle mass to the total mass of soft tissue is 0.26 in *A. colbecki*, only about half the ratio found in the tropical scallop, 0.53. As a result, the adductor muscle in *A. colbecki* forms only 16% of the total mass of the organism, less than the 26% found in the tropical scallop.

#### Power-to-mass ratio

If the mass-specific power output of the muscle were constant, the ratio of muscle mass to weight in water would be an index of power available for swimming relative to the weight that must be lifted. This ratio is  $0.061 \text{ s}^2 \text{ m}^{-1}$  in the Antarctic scallop, 79% of the corresponding value for the tropical scallop,  $0.077 \text{ s}^2 \text{ m}^{-1}$ . However, as noted previously, Bailey et al. showed that both contraction speed and maximum tension of *A. colbecki* muscle are half that of a temperate scallop (*Argopecten irradians*) (Bailey et al., 2005). Because power is equal to the product of force and velocity, the reduced speed and tension found in the Antarctic scallop suggest that the mass-specific power output of *A. colbecki* muscle is only about 25% that of a temperate scallop. If this is so, the ratio of power to weight in *A. colbecki* is only about 20% that of its temperate and tropical relatives. The resulting reduction in capability is evident in the slow swimming speed of *A. colbecki* (Ansell et al., 1998; Bailey et al., 2005), a speed apparently just sufficient to keep the animal aloft (Cheng and DeMont, 1996). In summary, *A. colbecki* has not effectively compensated for the effects of low temperature on its adductor muscle's power output by increasing the mass of the muscle relative to that of the shell.

#### Resonant frequency

The clapping frequency of *A. colbecki* is indistinguishable from the shell's resonant frequency, suggesting that, as with temperate scallops (DeMont, 1990), the Antarctic scallop may reduce the cost of locomotion by tuning its swimming to the oscillatory mechanics of its shell-hinge system.

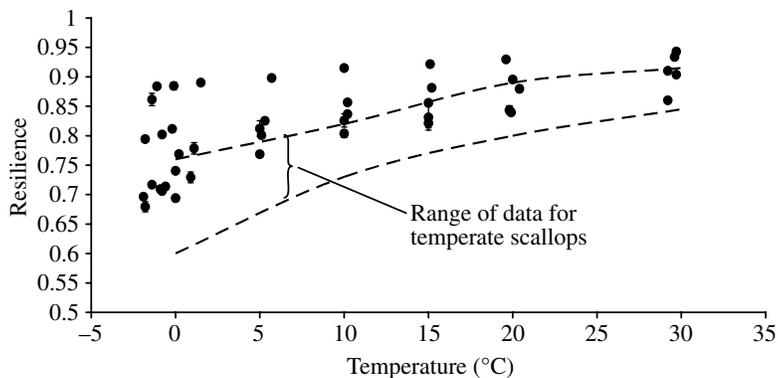


Fig. 8. The resilience of *A. colbecki* abductin as a function of temperature. The broken lines show the range of values measured on a temperate scallop (Bowie et al., 1993). Error bars are 95% confidence limits.

Table 1. Symbols used in the text, and the equation in which they first appear

| Symbol     | Definition                             | Units                        | Equation |
|------------|----------------------------------------|------------------------------|----------|
| $a$        | Area                                   | m <sup>2</sup>               | –        |
| $A_i$      | Amplitude                              | rad                          | –        |
| $B$        | Slope                                  | (half cycle #) <sup>-1</sup> | 4        |
| $E$        | Elastic modulus                        | Pa                           | 11       |
| $F$        | Applied force                          | N                            | 8        |
| $F_R$      | Resistive force                        | N                            | 13       |
| $i$        | Half-cycle number                      | –                            | –        |
| $k$        | Slope                                  | –                            | 13       |
| $K_m$      | Stiffness of the muscle                | N rad <sup>-1</sup>          | 1        |
| $K_r$      | Stiffness of the resilium              | N rad <sup>-1</sup>          | 2        |
| $L$        | Length                                 | m                            | 8        |
| $m$        | Mass                                   | kg                           | 1        |
| $M_F$      | Applied moment                         | Nm                           | 12       |
| $M_R$      | Resistive moment                       | Nm                           | 14       |
| $P$        | Pressure                               | Pa                           | 9        |
| $R_s$      | System resilience                      | –                            | 6        |
| $R_a$      | Abductin resilience                    | –                            | –        |
| $S$        | Entropy                                | JK <sup>-1</sup>             | 8        |
| $T$        | Absolute temperature                   | K                            | 8        |
| $t_d$      | Resonant period                        | s                            | A3       |
| $t_{inf}$  | Inflation time                         | s                            | 2        |
| $t_{jet}$  | Jet time                               | s                            | 1        |
| $U$        | Internal energy                        | J                            | 8        |
| $V$        | Volume                                 | m <sup>3</sup>               | 8        |
| $X_F$      | Moment arm of applied force            | m                            | 12       |
| $x$        | Moment arm                             | m                            | 13       |
| $x_{max}$  | Maximum moment arm in resilium         | m                            | –        |
| $\delta$   | Logarithmic decrement (per half cycle) | –                            | 4        |
| $\delta_e$ | Logarithmic decrement (per full cycle) | –                            | –        |
| $\lambda$  | Compression ratio                      | –                            | 9        |
| $\zeta$    | Damping coefficient                    | –                            | 1        |
| $\sigma$   | Stress                                 | MPa                          | 11       |
| $\omega_n$ | Natural radian frequency               | rad <sup>-1</sup>            | A1       |
| $\omega_d$ | Damped radian frequency                | rad <sup>-1</sup>            | A2       |

### Rotational stiffness

The rotational stiffness of the specimens measured here (0.034 Nm rad<sup>-1</sup>) is less than that measured for temperate scallops 0.16–0.29 Nm rad<sup>-1</sup> [*Argopecten irradians* and *Pecten maximus*, respectively (DeMont, 1990)]. Although this comparison is based on only a few samples of each species, it does not seem that *A. colbecki* has increased (or even maintained) its rotational stiffness. Further evidence is provided by the resonant frequency of the shell, noted above. If *A. colbecki* had the same rotational stiffness as temperate scallops, it would have a higher resonant frequency of oscillation due to its smaller shell (Eqn 3). Instead, its resonant frequency (1.45–2.00 Hz) is comparable to that of *P. maximus* [1.4–2.7 Hz (DeMont, 1990)].

Table 2. Results of the comparison of resilience between the Antarctic and temperate scallops

| Source                | SS    | d.f. | MS    | F ratio | P      |
|-----------------------|-------|------|-------|---------|--------|
| Temperature           | 0.214 | 5    | 0.043 | 28.376  | <0.001 |
| Species               | 0.046 | 1    | 0.046 | 30.372  | <0.001 |
| Temperature × species | 0.013 | 5    | 0.003 | 1.662   | 0.156  |
| Error                 | 0.101 | 67   | 0.002 |         |        |

### Stiffness of abductin

The elastic modulus of *A. colbecki* is 1.7–4.6 MPa, depending on temperature and compression ratio. Trueman (Trueman, 1953) and Alexander (Alexander, 1966) measured similar moduli (3 and 4 MPa, respectively) for temperate scallops, and moduli in this range are typical for biological rubbers in general (Wainwright et al., 1974). Thus, *A. colbecki* has not adjusted to the cold by substantially increasing the stiffness of its abductin.

### Resilience of abductin

At low temperature, *A. colbecki* abductin is more resilient than that of temperate scallops, and this resilience contributes to maintaining the damping coefficient for the shell-hinge system at a practical level. The damping coefficient for the oscillating shell (0.215) is similar to the value of 0.2 estimated by DeMont (DeMont, 1990) for a temperate scallop. In both cases, the damped resonant frequency (and thereby the power available for thrust) is only about 2% lower than that in the total absence of damping (Eqn 3).

However, it is difficult to judge the importance of this increase in resilience. First, as noted previously, most of the energetic loss during oscillation of a scallop shell is due to hydrodynamics, not to the resilium's abductin. For example, at 8°C, the resilience of *A. colbecki* abductin is about 0.86 (Fig. 8). Thus, 1–0.86=14% of the elastic potential energy stored in a fully compressed resilium is lost in each cycle of oscillation due to viscous interactions within the resilium itself. By contrast, the resilience of the whole-shell system tested at this temperature was 0.252, implying that ~75% of the initial elastic potential energy stored in the resilium is lost when the system oscillates in water. Apparently, in a cycle, 61% (14–75%) of the initial energy is lost due to hydrodynamics, about 4.4 times the amount lost to abductin. As a consequence, any change in the resilience of abductin can cause only a relatively small change in the overall resilience of the shell-hinge system.

Furthermore, even drastic changes in the resilience of abductin would make only small changes in the resonant period of the shell-hinge system, and therefore in the power of thrust. For example, a decrease in the resilience of abductin from 0.86 to 0.72 would double the fraction of energy lost in the hinge, from 14% to 28% of the total. When this energy loss is added to the 61% of energy lost to hydrodynamics, 89% of the initial elastic energy stored in this hypothetical low-resilience shell would be lost in each cycle ( $R_s=0.11$ ), increasing the damping

Table 3. Planned comparisons between the resilience of *A. colbecki* and that of a temperate scallop at various temperatures

| Temperature (°C) | Source     | SS    | d.f. | MS    | F ratio | P      |
|------------------|------------|-------|------|-------|---------|--------|
| 0                | Hypothesis | 0.030 | 1    | 0.030 | 19.829  | <0.001 |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |
| 5                | Hypothesis | 0.016 | 1    | 0.016 | 10.373  | 0.002  |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |
| 10               | Hypothesis | 0.010 | 1    | 0.010 | 6.574   | 0.013  |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |
| 15               | Hypothesis | 0.002 | 1    | 0.003 | 1.758   | 0.189  |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |
| 20               | Hypothesis | 0.001 | 1    | 0.002 | 1.425   | 0.237  |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |
| 30               | Hypothesis | 0.001 | 1    | 0.001 | 0.987   | 0.324  |
|                  | Error      | 0.101 | 67   | 0.002 |         |        |

coefficient from 0.215 to 0.331 (Eqn 7). However, this substantial increase in  $\zeta$  results in only a minor decrease in the power available for thrust (Eqn 3): 5.6% less than that of a totally undamped system vs 2.3% for the system as it exists now. It would thus seem that the resilience of abductin, even in the cold, plays a small role in scallop locomotion.

However, as we have seen, *A. colbecki* is underpowered relative to temperate scallops and perhaps on the verge of not being able to swim. As a result, even small changes in overall damping (and therefore in the power available for thrust) might be important. We are forced to speculate that the effects of abductin resilience at low temperatures, small as they might be,

have been sufficient to select for the increased resilience seen in this species.

If abductin has evolved in response to a small selective pressure at low temperature, why the lack of effective adaptation in other parts of the locomotory system? Definitive answers are not yet available, but speculation is again possible. Bailey et al. (Bailey et al., 2005) suggest that the reduction in shell mass may be a response to release from predation: crabs, a potent selective factor in many aspects of shell morphology (Vermeij, 1993), are absent from the high Antarctic, and other predators (such as sea stars) may move so slowly that an energetic escape response is not necessary. Shell reduction

Table 4. Amino acid composition (mol%) of scallop abductin

| Amino Acid    | <i>A. col.</i> | 95% CL | <i>Aeq. ir.</i> | <i>Pl. mag.</i> | <i>Pec. max.</i> | Mean  | 95% CL |
|---------------|----------------|--------|-----------------|-----------------|------------------|-------|--------|
| Glycine       | 70.74          | 12.72  | 68.39           | 67.85           | 63.02            | 66.42 | 5.43   |
| Methionine    | 10.21          | 10.89  | 5.96            | 8.87            | 16.28            | 10.37 | 9.78   |
| Aspartic acid | 4.94           | 1.69   | 8.6             | 5.12            | 5.50             | 6.41  | 3.98   |
| Phenylalanine | 4.11           | 1.82   | 6.02            | 2.86            | 3.80             | 4.23  | 3.51   |
| Alanine       | 2.06           | 1.55   | 1.71            | 6.02            | 3.44             | 3.72  | 0.83   |
| Serine        | 1.81           | 1.19   | 2.96            | 2.16            | 2.19             | 2.44  | 2.98   |
| Lysine        | 1.38           | 1.15   | 1.3             | 1.83            | 1.67             | 1.60  | 0.42   |
| Arginine      | 1.35           | 0.04   | .86             | 1.27            | 0.88             | 1.00  | 0.54   |
| Glutamic acid | 0.91           | 0.26   | 1.10            | 0.59            | 0.96             | 0.88  | 0.50   |
| Proline       | 0.84           | 0.12   | 1.05            | 0.59            | 0.58             | 0.74  | 0.48   |
| Leucine       | 0.52           | 0.59   | 0.41            | 0.88            | 0.35             | 0.55  | 0.11   |
| Threonine     | 0.38           | 0.15   | 0.64            | 0.32            | 0.47             | 0.48  | 0.49   |
| Lisoleucine   | 0.34           | 0.28   | 0.47            | 0.20            | 0.44             | 0.37  | 0.29   |
| Valine        | 0.16           | 0.09   | 0.11            | 0.84            | 0.09             | 0.35  | 0.27   |
| Cysteine      | 0.15           | 0.34   | 0.19            | 0.23            | 0.31             | 0.24  | 0.34   |
| Tyrosine      | 0.10           | 0.05   | 0.24            | 0.37            | 0                | 0.20  | 0.79   |
| Histidine     | 0              | 0      | 0               | 0               | 0                | 0     | 0      |
| Tryptophan    | 0              | 0      | 0               | 0               | 0                | 0     | 0      |

Data for *Aequipecten irradians* (*Aeq. ir.*) and *Placopecten magellanicus* (*Pl. mag.*) are from Kahler et al. (Kahler et al., 1976). The values for *A. colbecki* (*A. col.*) and *Pecten maximus* (*Pec. max.*) are the mean among the three samples. For comparison, the mean among the three temperate and tropical species is given.

Table 5. Bray–Curtis similarity matrix for scallop abductins, expressed as percent

|                  | <i>A. col.</i> 1 | <i>A. col.</i> 2 | <i>A. col.</i> 3 | <i>Aeq. ir.</i> | <i>Pl. mag.</i> | <i>P. max.</i> |
|------------------|------------------|------------------|------------------|-----------------|-----------------|----------------|
| <i>A. col.</i> 1 | 100              |                  |                  |                 |                 |                |
| <i>A. col.</i> 2 | 90.79            | 100              |                  |                 |                 |                |
| <i>A. col.</i> 3 | 90.44            | 83.84            | 100              |                 |                 |                |
| <i>Aeq. ir.</i>  | 89.84            | 86.14            | 90.47            | 100             |                 |                |
| <i>Pl. mag.</i>  | 96.58            | 88.95            | 89.50            | 90.47           | 100             |                |
| <i>P. max.</i>   | 93.65            | 88.34            | 88.05            | 95.23           | 95.23           | 100            |

The three samples from *A. colbecki* (*A. col.*) are no more similar to each other than they are to the three temperate species: *Aeq. ir.*, *Aequipecten irradians*; *Pl. mag.*, *Placopecten magellanicus*; *P. max.*, *Pecten maximus*.

resulting from release from predation could be compounded by the difficulty of maintaining a calcium-carbonate shell in the cold waters of Antarctica (Vermeij, 1993): calcium carbonate is substantially more soluble in cold water than in warm water. Thus, it is possible that the reduction in shell mass in *A. colbecki* is not tied to locomotion alone.

If shell mass were reduced at least in part for non-locomotory reasons, it might explain the apparently maladaptive reduction in muscle mass noted here. The shell of *A. colbecki* is extremely fragile. If the adductor muscle were to pull harder or faster than it does on this fragile shell, the shell might break. We picture a scenario in which shell mass is reduced in response to a variety of selective pressures, requiring in turn a reduction in muscle mass, a reduction abetted by concomitant reduction in metabolic energy demand of the muscle. In turn, reduced muscle mass creates a selection pressure (albeit probably a small one) for increased resilience in the shell's hinge.

#### Amino acid composition

Regardless of its evolutionary history, the increased resilience of *A. colbecki* abductin is intriguing. A rubber that retains its resilience at low temperature would be of practical value for human technology, and it will therefore be useful to determine the molecular basis for the increased resilience in *A. colbecki* abductin. However, the amino acid composition of *A. colbecki* abductin is very similar to that of temperate scallops (Table 4), indicating that compositional adjustments to cold temperatures are subtle.

For example, it is possible that the ratio of methionine to methionine sulfoxide is higher in *A. colbecki* than in temperate scallops: methionine is more hydrophobic than methionine sulfoxide, and the weakening of any hydrophobic interactions at low temperature would help maintain the mobility of protein chains. However, the analysis performed here does not distinguish between methionine and methionine sulfoxide: both are converted to methionine sulfone before hydrolysis.

One other protein rubber, elastin, is known to maintain high resilience at low temperature (Gosline and French, 1979). As temperature decreases, hydrophobic bonds within the elastin rubber network weaken and the rubber swells drastically,

thereby reducing viscous interactions among chains. However, if this mechanism is present in *A. colbecki* abductin, its action must be relatively subdued: unlike elastin, *A. colbecki* abductin volume decreases at low temperatures.

#### Conclusion

A variety of strategies have been available to *A. colbecki* to maintain its swimming ability in the cold waters of Antarctica. However, its abductin is no stiffer than that of temperate and tropical scallops, and a substantial reduction in shell mass is more than offset by a drastic reduction in adductor-muscle mass. This appears to leave an increase in abductin resilience as the operative adaptation. This conclusion is less than satisfying, though, because the beneficial effects of increased resilience are so small. Regardless of its evolutionary history, the increased resilience of *A. colbecki* abductin may be of interest to materials engineers.

#### Appendix 1

Damping coefficient and logarithmic decrement are related through the following equations (Thomson, 1986):

$$\omega_n = \frac{\omega_d}{\sqrt{1 - \zeta^2}}, \quad (\text{A1})$$

$$\omega_d = \frac{2\pi}{t_d}, \quad (\text{A2})$$

$$\delta_e = \zeta \omega_n t_d. \quad (\text{A3})$$

Here,  $\omega_n$  is the natural radian frequency of the system,  $\omega_d$  is its damped frequency,  $\delta_e$  is the full-cycle logarithmic decrement,  $t_d$  is the damped period, and  $\zeta$  is the damping coefficient. Inserting Eqn A2 into Eqn A1, we see that:

$$\omega_n = \frac{2\pi}{t_d \sqrt{1 - \zeta^2}}. \quad (\text{A4})$$

Inserting Eqn A4 into Eqn A3, and noting that  $\delta_e = 2\delta$ , we arrive at the conclusion that:

$$\delta = \frac{\pi \zeta}{\sqrt{1 - \zeta^2}}. \quad (\text{A5})$$

Solving for  $\zeta$  leads us to the final result:

$$\zeta = \frac{1}{\sqrt{\frac{\pi^2}{\delta^2} + 1}}. \quad (\text{A6})$$

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