

## SHORT COMMUNICATION

### DAMPING IN THE HINGE OF THE SCALLOP *PLACOPECTEN* *MAGELLANICUS*

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The family Pectinaceae are the only bivalves that have been well documented as swimmers (DeMont, 1992), although *Ensis minor* has been observed to swim (McMahon and McMahon, 1983). The behaviour was once regarded only as an escape response (Gäde, 1981; McMahon and McMahon, 1983), but some studies suggest seasonal migrations are involved (Gruffydd, 1976; DeMont, 1990). DeMont (1990) suggests that they swim at the natural frequency of the shell-hinge system for more efficient use of energy.

The family Pectinaceae have acquired the ability to swim through the development of a specialized hinge ligament (Trueman, 1953*a,b*; DeMont, 1992). The hinge ligament is made up of two parts: the inner and outer ligaments. The inner ligament is located ventrally and acts as a compression spring that forces the shells apart when the adductor muscle relaxes (Alexander, 1966). The outer ligament is located dorsally and connects the two valves, acting as a tension spring when the valves are closed. In other bivalves, such as *Mytilus*, *Ostrea* or *Tellina*, the inner hinge ligament is calcified throughout, but in *Pecten magellanicus* it is only calcified at the fusion layer, where it attaches to the shell (Trueman, 1953*a,b*; Alexander, 1966; DeMont, 1992). The material that comprises the inner hinge ligament, abductin, is one of the few known biomaterials that exists as a one-phase amorphous polymer system (Wainwright *et al.* 1982). Abductin is different from other rubber-like proteins in that it contains large amounts of the amino acid methionine, while the other materials contain little or none (Kahler *et al.* 1976; Wainwright *et al.* 1982).

For such a hinge to function efficiently as a spring, it must be compliant enough to be deformed by the muscle and have a low energy loss, or damping, at functional frequencies. Alexander (1966) showed that the elasticity of the inner hinge ligament is mainly due to entropy changes, but no studies have quantified the mechanical properties of the intact hinge over normal physiological conditions. In this study, the damping of

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intact scallop hinges was measured over physiological ranges of swimming frequencies and environmental temperatures.

Scallops [*Placopecten magellanicus* (Gmelin)] were obtained from a fisherman at Wood Islands, Prince Edward Island. The scallops used ranged from 82.5 to 208.1g in wet mass. They were maintained in a large aquarium with recirculating sea water and kept at 10°C. They were cared for and disposed of following the principles of The Canadian Council of Animal Care. Before any tests were initiated, the scallops were killed and weighed on a digital balance scale (Mettler PJ3600). The maximum *in vivo* gape was measured using a Vernier caliper (Mitutoyo) and the scallop was then eviscerated. The empty intact valves were then weighed. All lengths are expressed in millimetres and all masses are expressed in grams.

Free damped oscillation tests were performed to quantify the damping of the intact hinge. The tests were carried out on a total of 14 animals, with a total of 212 trials. Holes were drilled in the top and bottom valves prior to the experiments. The hole in the bottom (right) valve was drilled in the area of contact of the valve and was used to secure the animal to a platform. Weights were mounted on a bolt inserted in the hole in the top (left) valve. This hole was drilled approximately 20mm from the ventral edge. This closed the valves to the maximum gape that had been measured before evisceration and, coincidentally, provided a free vibration frequency of about 3Hz. We did not attempt to vary the free vibration frequency by varying the added mass, but chose to standardize tests by ensuring that the amplitudes of the oscillations were always physiological. A video dimension analyzer (VDA) (model 303, Instrumentation for Physiology and Medicine Inc., San Diego) was used to record the free damped oscillations. The device was set up to measure the displacement of the freely oscillating top valve by triggering off the leading edge of the valve. The VDA produced an analog output that was collected on a digitizing oscilloscope (HP54501A). The data were digitized, stored on disc and analyzed using Asystant (Asyst Software Technologies, Inc.). The wave envelope was fitted to an exponential curve of the form  $y = e^{ax+b}$ . The values of  $a$ ,  $b$  and the frequency of oscillation were used to calculate the natural logarithmic decrement ( $\Delta$ ), which is the natural logarithm of the ratio of successive amplitudes (Thompson, 1988). Several methods of describing elastic efficiency are used in the literature and are related by the following equation (Alexander, 1966):

$$\ln \left( \frac{100}{R} \right) = \pi \tan \delta = 2\Delta,$$

where  $R$  is the resilience and  $\tan \delta$  is the loss tangent, which is frequently calculated in experiments where transient strains are applied (Wainwright *et al.* 1982). The tests were carried out over a range of temperatures from  $-4^\circ\text{C}$  to over  $80^\circ\text{C}$  to measure any temperature dependence on damping. Single measurements of the free damped oscillations were made at each temperature. The tests were initiated at room temperature, then increased to  $80^\circ\text{C}$  by increments of about  $5^\circ\text{C}$ . The temperature was then reduced to  $0^\circ\text{C}$  by the same temperature increments and finally increased again to room temperature. This protocol verified that no physical changes in the hinge were caused by the

temperature changes. Water was periodically applied to the ligament to maintain the hydration of the hinge.

For the tests at temperatures above room temperature, the right valve of the scallop was mounted on a reinforced pan covered with a Plexiglas container. The hydration of the hinge was maintained by the addition of water to the pan. The apparatus was placed inside a commercially available toaster oven with a glass door that could be used as a viewing window. For the tests at temperatures below room temperature, the entire apparatus was placed in a refrigerated cabinet modified to hold the apparatus. The data were collected and analyzed using the same methods as those used for the tests above room temperature. All temperatures were measured using an Omega DP30 digital thermometer.

Viscoelastic materials exhibit frequency and temperature dependence in some of their mechanical properties, depending on the region of the response curve in which they are functioning. It is necessary to quantify this dependency at physiological frequencies and temperatures to understand the importance of the elastic mechanism in the locomotion of these animals. Free damped oscillation tests were performed on scallop hinges to test for any dependence of damping on temperature. Cross-linked amorphous polymers working in the pseudo-equilibrium zone, such as abductin at physiological frequencies (Alexander, 1966), should have frequency-independent loss tangents (Ferry, 1961), so we did not systematically examine the effect of frequency dependency on damping. Fig. 1 is an example of a free damped oscillation. The scallop used in this trial weighed 130.4 g and this trial was performed at 17.8°C. The fitted wave envelope is shown on the top half of the curve and the slope of the exponentially decaying curve was used to calculate the natural logarithmic decrement. Fig. 2 is a graph of the cumulative results of the free damped oscillations, with the resilience plotted against temperature. This demonstrates

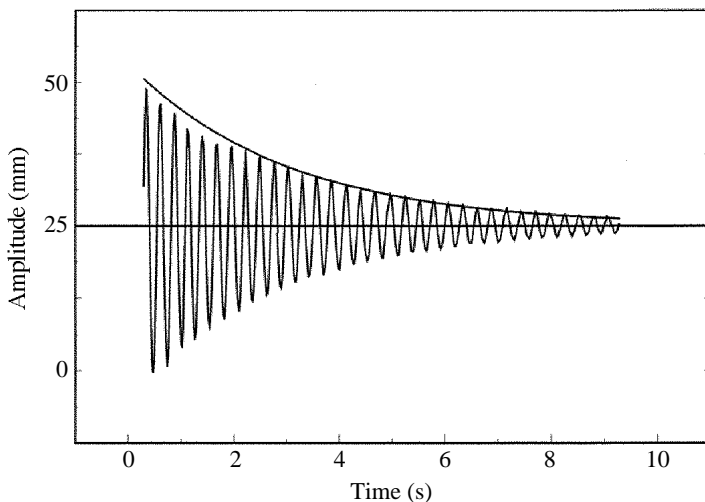


Fig. 1. A graph of a free damped oscillation with the amplitude of the maximum gape of the shell plotted against time. The graph shows the digitized output of the VDA. The fitted exponential decay curve is also shown on the graph. The scallop used in this trial weighed 130.4g and the temperature was 17.8°C.

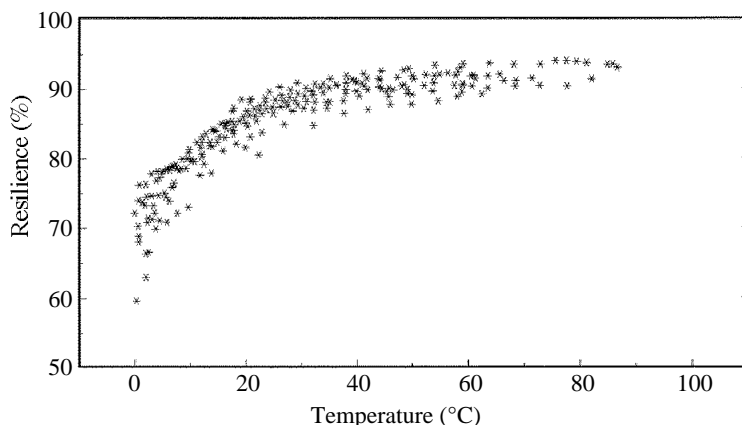


Fig. 2. Cumulative results of the free damped oscillation tests, with resilience plotted against temperature. There were a total of 14 animals and 212 trials used in these tests, over temperatures ranging from 0°C to 87°C and each point represents one trial.

the dependence of damping on temperature, showing that the ligament loses much more energy at low temperatures than at high temperatures.

Two types of swimming are used by aquatic animals: (1) appendage-based swimming and (2) jet propulsion. Appendage-based swimming involves the displacement of a large volume of water at low velocities, while jet propulsion involves the displacement of small volumes of water at high velocities. Thus, the Froude efficiency of jet propulsion is low (Alexander, 1977). Jet propulsion functions by the intake of water into a region of variable volume. Water is forced out of the cavity following contraction of locomotor muscles to form a jet. In scallops, the variable volume is the space between the shells, which are joined at one end by the hinge. This hinge functions elastically to antagonize the contraction of the locomotor muscle and powers the refilling phase of the jet cycle. In order for this mechanism to function properly, the hinge must be capable of efficiently storing and recovering elastic strain energy. Clearly, the mechanical properties of the hinge should be incorporated as an important component of bioenergetic models of scallops, some of which are commercially important. Some researchers believe that scallops not only swim to escape predation but move in seasonal migrations (Dadswell and Weihs, 1990), possibly to locate more suitable habitats (Gruffydd, 1976; Winter and Hamilton, 1985). We have now measured one mechanical property of the scallop hinge, with experimental conditions that simulate natural conditions and present the results in this paper.

We quantified damping, a functionally important mechanical property of intact hinges. Damping was measured from free damped oscillations performed over temperatures of below  $-5^{\circ}\text{C}$  to temperatures of over  $85^{\circ}\text{C}$ . The scallop actually lives at temperatures from around  $4^{\circ}\text{C}$  to above  $20^{\circ}\text{C}$  (Johannes, 1957). The damping was temperature-dependent, increasing as temperature decreased; at  $10^{\circ}\text{C}$  the resilience of the intact hinge was about 79%. At temperatures below the freezing point of water, the abductin cannot

be expected to function normally and our unpublished results showed that damping increased dramatically.

We have shown that the amount of energy recovered is dependent on temperature. This information will be important in bioenergetic models that incorporate the costs of locomotion. However, information about two important components is still required. The first required component is quantification of the energetics of the muscle during physiological conditions. Recently, Marsh *et al.* (1992) have made remarkable measurements of the *in vivo* mechanical properties of the adductor muscle. The second, and possibly more difficult component to evaluate, is the effect of the unsteadiness of the locomotion on the production of the acceleration reaction (Daniel, 1984). This requires knowledge of the added mass coefficients of oscillating flat plates, which is not currently available.

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### References

- ALEXANDER, R. MCN. (1966). Rubber-like properties of the inner hinge ligament of Pectinidae. *J. exp. Biol.* **4**, 119–130.
- ALEXANDER, R. MCN. (1977). Swimming. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander and G. Goldspink), pp. 222–247. London: Chapman and Hall.
- DADSWELL, M. J. AND WEIS, D. (1990). Size-related hydrodynamic characteristics of the giant scallop, *Placopecten magellanicus* (Bivalvia: Pectinidae). *Can. J. Zool.* **68**, 778–785.
- DANIEL, T. L. (1984). Unsteady aspects of aquatic locomotion. *Am. Zool.* **24**, 121–134.
- DEMONT, M. E. (1990). Tuned oscillations in the swimming scallop *Pecten maximus*. *Can. J. Zool.* **68**, 786–791.
- DEMONT, M. E. (1992). Locomotion of soft bodied animals. In *Advances in Comparative and Environmental Physiology*, vol. 11 (ed. R. McN. Alexander), pp. 167–190. Berlin: Springer-Verlag.
- FERRY, J. D. (1961). *Viscoelastic Properties of Polymers*. New York: John Wiley & Sons, Inc.
- GÅDE, G. (1981). Energy production during swimming in the adductor muscle of the bivalve *Limahians*: comparison with the data from other bivalve mollusks. *Physiol. Zool.* **54**, 400–406.
- GRUFFYDD, L. D. (1976). Swimming in *Chlamys islandica* in relation to current speed and an investigation of hydrodynamic lift in this and other scallops. *Norw. J. Zool.* **24**, 365–378.
- JOHANNES, R. E. (1957). High temperatures as a factor in scallop mass mortalities. *Fisheries Research Board of Canada*. Manuscript 638.
- KAHLER, G. A., FISHER, F. A. AND SASS, R. L. (1976). The chemical composition and mechanical properties of the hinge ligament in bivalve molluscs. *Biol. Bull. mar. biol. Lab., Woods Hole* **151**, 161–181.
- MARSH, R. L., OLSON, J. M. AND GUZIK, S. K. (1992). Mechanical performance of scallop adductor muscle during swimming. *Nature* **357**, 411–413.
- MCMAHON, R. F. AND MCMAHON, C. O. (1983). Leaping and swimming as predator escape responses in the jackknife clam, *Ensis minor* Dall (Bivalvia: Pharellidae). *Nautilus* **93**, 55–58.
- THOMPSON, W. T. (1988). *Theory of Vibrations With Applications*, third edition. Englewood Cliffs, NJ: Prentice Hall.
- TRUEMAN, E. R. (1953a). Observations on certain mechanical properties of the ligament of *Pecten*. *J. exp. Biol.* **30**, 453–467.
- TRUEMAN, E. R. (1953b). The ligament of *Pecten*. *Q. Jl microsc. Sci.* **94**, 193–202.
- WAINWRIGHT, S. A., BIGGS, W. D., CURREY, J. D. AND GOSLINE, J. M. (1982). *Mechanical Design in Organisms*. Princeton, NJ: Princeton University Press.
- WINTER, M. A. AND HAMILTON, P. V. (1985). Factors influencing swimming in bay scallops, *Argopecten irradians* (Lamarck, 1819). *J. exp. mar. Biol. Ecol.* **88**, 227–242.