

Biomechanics of byssal threads outside the Mytilidae: *Atrina rigida* and *Ctenoides mitis*

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Accepted 27 February 2009

SUMMARY

The byssus is the set of proteinaceous threads widely used by bivalves to attach themselves to the substrate. Previous researchers have focused on a single byssate family, the Mytilidae. However, the properties of byssal threads from species outside this family are of interest – first, because evolutionary patterns are only detectable if species from a range of taxa are examined, and second, because recent biomimetic research efforts would benefit from a wider range of ‘mussel glue’ exemplars. In the present study, we measured the mechanical properties of the byssal threads of two species outside the Mytilidae, the pen shell *Atrina rigida* Lightfoot and the flame ‘scallop’ *Ctenoides mitis* Lamarck. The mechanical properties of their byssal threads were significantly different from those of mytilids. For instance, the byssal threads of both species were significantly weaker than mytilid threads. *Atrina rigida* threads were significantly less extensible than mytilid threads, while *C. mitis* threads exhibited the highest extensibility ever recorded for the distal region of byssal threads. However, there were also interesting similarities in material properties across taxonomic groups. For instance, the threads of *A. rigida* and *Modiolus modiolus* Linnaeus both exhibited a prominent double-yield behavior, high stiffness combined with low extensibility, and similar correlations between stiffness and other thread properties. These similarities suggest that the thread properties of some semi-infaunal species may have evolved convergently. Further research on these patterns, along with biochemical analysis of threads which exhibit unusual properties like double-yield behavior, promises to contribute to both evolutionary biology and materials engineering.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/212/10/1449/DC1>

Key words: byssus, byssal threads, *Atrina rigida*, *Ctenoides mitis*, biomechanics, material properties.

INTRODUCTION

According to Tertullian (*ca.* 155–230 CE), it was not always possible to find sufficient earthly textiles; luckily, it ‘also proved possible to fish for clothes’. He goes on to say that ‘fleeces also come from the sea’ (Tertullian, 2005). Though he may have had his tongue held firmly in cheek, Tertullian’s ‘fleeces of the sea’ were the byssal threads of *Pinna nobilis* Linnaeus which, at least by the 18th century, actually were sometimes woven into hats and gloves (Maeder, 2002).

Despite such interesting historical uses, no work in the last 50 years has investigated the mechanical properties of pinnid byssal threads [the most recent study is by Lucas and colleagues (Lucas et al., 1955)]. Instead, most byssal research to date has focused on the byssal threads of mytilids (mussels and their near relatives). This disproportionate emphasis on the Mytilidae is likely due to the presence of mytilids in easily accessible intertidal areas, but it fails to capture the widespread occurrence of byssal attachment among the Bivalvia and the potential diversity in byssal function and properties.

Although the byssus first evolved to aid in post-larval dispersal and settlement (Yonge, 1962; Stanley, 1972; Sigurdsson et al., 1976; De Blok and Tan-Maas, 1977; Lane et al., 1985), a recent catalogue of tropical marine bivalves revealed that about a quarter of the genera surveyed are byssally attached as adults (Todd, 2001). In fact, the only pteriomorph superfamilies without byssate adult representatives are characterized by a different attachment strategy – cementation (Márquez-Aliaga et al., 2005; Bieler and Mikkelsen, 2006).

Although there has been some research into non-mytilid byssal thread chemical composition, *Dreissena polymorpha* Pallas is the only bivalve from outside the Mytilidae whose threads have been the subject of biomechanical investigation (Jackson et al., 1953; Pujol, 1967; Pujol et al., 1970; Mascolo and Waite, 1986; Brazee and Carrington, 2006).

Biomechanics researchers have thus restricted their study of an attachment structure that appears in every pteriomorph order to only a single family. This narrow focus is a problem that should be remedied, for two reasons: first, because of the phenomenon of phylogenetic non-independence, many interesting evolutionary questions can only be answered through comparative work across a wide range of taxa; and second, as researchers have pointed out the possible engineering applications of simulated ‘mussel glue’, knowledge of a wider range of byssal thread compositions and properties is likely to yield rich insights into potential technological applications (Waite et al., 2005; Waite, 2008).

With more biomechanical data on the threads of both epifaunal and semi-infaunal bivalves from a variety of pteriomorph orders, one would be able to sort out whether life habits are correlated with the mechanical properties of byssal threads. This is an especially interesting question, as both endobysate (infaunal or semi-infaunal with byssal attachment) and epibysate (epifaunal with byssal attachment) groups declined during the Paleozoic and Mesozoic, perhaps due to increased predation pressure (Stanley, 1972; Stanley, 1977; Vermeij, 1983; Skelton et al., 1990; Aberhan et al., 2006; Harper, 2006). The surviving byssate groups live in a variety of

environments, and their survival probably involved adjustments of their thread mechanics. There are certainly interesting chemical differences between the threads of different bivalve groups, which may translate into differences in mechanical properties. For example, mytilid threads are collagenous, whereas the threads of pinnids, anomniids and dreissenids are not (Jackson et al., 1953; Pujol, 1967; Pujol et al., 1970; Mascolo and Waite, 1986; Brazee and Carrington, 2006).

We investigated the mechanical properties of the byssal threads of two bivalve species from two orders outside the Mytiloidea: the pen shell *Atrina rigida* Lightfoot (Pterioidea: Pinnidae) and the flame 'scallop' *Ctenoides mitis* Lamarck (Limoida: Limidae). There is some debate in the literature about the breakdown of pteriomorph orders; we have adopted the classifications of Bieler and Mikkelsen rather than those of Matsumoto but these authors all agree that limids and pinnids belong to different orders (Matsumoto, 2003; Bieler and Mikkelsen, 2006). Thus, although *A. rigida* and *C. mitis* are more closely related to one another than to mytilid species, they are still only distantly related. This study does not seek to compare mytilid threads with 'non-mytilid' threads in general but instead compares mytilid threads with the threads of two unrelated species from outside the Mytilidae.

The two species under investigation have quite different life habits – *A. rigida* is semi-infaunal, and usually lives in protected subtidal or low intertidal areas with most of its shell buried in muddy or sandy sediment; *C. mitis*, in contrast, is epifaunal, and normally lives byssally attached in crevices of reefs and ledges, swimming only if disturbed (Stanley, 1970; Mikkelsen and Bieler, 2003). Because *A. rigida* is semi-infaunal, data on the properties of its threads can be compared with data from our recent study that includes two semi-infaunal mytilids, *Modiolus modiolus* Linnaeus and *Geukensia demissa* Dillwyn [see accompanying paper (Pearce and LaBarbera, 2009)]. The properties of epifaunal *C. mitis* threads can similarly be compared with those of epifaunal mytilids like *Mytilus californianus* Conrad and *Mytilus edulis* Linnaeus (Pearce and LaBarbera, 2009).

MATERIALS AND METHODS

Atrina rigida Lightfoot specimens were ordered from Gulf Specimen Marine Laboratories (Panacea, FL, USA), and kept in a tank at room temperature (approximately 18°C). We buried them as deeply as possible (~5 cm) in the calcareous gravel in the aquarium, and lightly supported the exposed shell to prevent toppling. *Ctenoides mitis* Lamarck specimens were ordered from Ward's Natural Science (Rochester, NY, USA) [the '*Lima scabra*' specimens obtained from Ward's were identified as *C. mitis* rather than *Ctenoides scaber* Born, following Mikkelsen and Bieler (Mikkelsen and Bieler, 2003), on the basis of their white tentacles and greater number of radial ribs in the shell]. The *C. mitis* were kept in individual enclosures (polyethylene freezer containers with sections of the walls replaced with plastic mesh) in the same tank as the *A. rigida* specimens. Tank salinity was maintained at approximately 31–32 p.p.t. by adding either tap water or Instant Ocean® (Aquarium Systems, Inc., Mentor, OH, USA) sea salt mixture as necessary. Animals were fed daily on an artificial phytoplankton substitute (Kent Marine®, PhytoPlex™, Franklin, WI, USA), producing byssal threads and surviving without obvious ill effects for over 2 months.

We measured the shell length of all animals using digital calipers. To harvest threads from the *C. mitis* specimens, we opened each enclosure and disturbed the animal inside, causing it to release its threads and swim away. We then lifted the enclosure out of the tank and removed the thread plaques from the plastic walls using a razor

blade. To harvest the *A. rigida* threads, we carefully dug out each animal and transferred it underwater into a smaller tray, which was then lifted out of the tank. We snipped each thread at the proximal end using iris scissors; the plaques usually remained attached to a small piece of gravel. All samples were stored in salt water (31–32 p.p.t.) at 5°C until testing.

Thread mechanical properties were measured using a custom-built tensile tester. The apparatus consisted of a lower grip at the bottom of a Plexiglas tank and an upper grip that could be displaced by turning a crank on a dovetail slider (Velmex, Bloomfield, NY, USA; Model A6027K1M-S6). The upper grip was attached to a 10 lb (~45 N full scale) force transducer (OmegaDyne®, Sunbury, OH, USA; Model LC703-10). The four strain gauges in the transducer were set up as a full Wheatstone bridge supplied with a constant 5 V excitation; the excitation and amplification of the voltage output of the bridge circuit were supplied by a bridge amplifier (Vishay® Micro-Measurements, Shelton, CT, USA; Model 2120A). We calibrated the voltage output of the amplifier to yield a voltage-to-force conversion factor. A linear variable differential transformer (Pickering Controls, Plainview, NY, USA; Model 7308-X2-A0) powered by a constant 5 V DC from an external power supply converted the displacement of the upper grip into a voltage, which could then be converted back into a displacement value following calibration. The voltage was digitized using a GW Instruments (Somerville, MA, USA) Model 100B analog-to-digital converter.

We limited each testing run to 10–15 byssal thread samples to minimize drying during preparation. Between one and six byssal threads from each individual were tested, with a total sample of about 20–25 threads per species. To ensure proper gripping, we sandwiched each end of each thread between two small squares of 100% rag paper using a drop of cyanoacrylate adhesive (Loctite® 'Gel Control' super glue; Henkel Consumer Adhesives, Inc., Avon, OH, USA) to maximize adhesion. Before testing, we measured the length of each byssal thread sample with digital calipers.

Prior to each test, we secured one end of the thread in the upper grip of the tester and the other end in the lower grip at the base of the tank; the entire thread was immersed in sea water for the duration of the test. The tank was filled with salt water from the 5°C tank (salinity 31–32 p.p.t.) during all tests. Once the thread was secured, we initiated data capture in the application instruNet World Mac (GW Instruments) and displaced the upper grip at approximately 0.5 mm s⁻¹ until thread failure. At the outset of the test, the samples were slack; the beginning of the tensile test was taken to be the point at which there was a non-negligible force on the sample.

Following testing, we inspected the broken ends of each byssal thread under a dissecting microscope to assess the failure mode (e.g. smooth break, fraying, etc.). We took digital photographs (Nikon D100 camera back) of each broken end through the dissecting microscope at approximately ×100, and measured thread diameter using ImageJ (NIH). Following previous work, cross-sections were assumed to be circular even though byssal threads are often elliptical in cross-section (Brazee and Carrington, 2006). Initially we measured the minimum thread diameter before testing, but discovered that the samples invariably broke at a different (and wider) location, presumably a cryptic weak point in the structure. Thus the diameter at failure was used in all calculations of strain to ensure consistency, although this does result in an underestimate of the inherent strength of byssal thread material.

The stress (force per unit area) and strain (displacement per unit length) for each test were plotted in Microsoft® Excel® to produce a stress–strain curve. Because strains were always in excess of 50%, it was clear that byssal thread cross-sectional area and length changed

significantly during the test. Thus instead of ‘engineering’ strain ($\epsilon_E = \Delta L/L_0$, where L is length and subscript 0 indicates initial) we used ‘true’ or ‘logarithmic’ strain [$\epsilon_T = \ln(L/L_0)$], which does not assume constant length or constant volume. Stress is always calculated assuming a certain value for Poisson’s ratio (ν), which is defined in this case as the negative of the ratio of transverse to axial strain. The instantaneous diameter of the thread is given by $d = d_0 \exp(-\nu \epsilon_T)$. There are two possible approaches. (1) ‘Engineering’ stress (σ_E) assumes constant area: $\nu = 0$, thus $d = d_0$ and $\sigma_E = F/A_0$ (where F is force and A is cross-sectional area). (2) ‘True’ stress (σ_T) assumes constant volume: $\nu = 0.5$, and $\sigma_T = \sigma_E \exp(\epsilon_T)$. We conservatively assumed constant volume rather than constant area (see Pearce and LaBarbera, 2009). A number of different mechanical properties can be determined from the stress–strain curve. In almost all cases, there was a sharp drop in stiffness at a characteristic stress level – the yield stress. The slope of the stress–strain curve represents the stiffness of the material; thread stiffness was determined both for the initial loading of the thread and at thread failure. The stress and strain at failure are termed strength and extensibility, respectively. Finally, by fitting a polynomial to the stress–strain curve and integrating over the total strain, the area under the curve was determined; this area is the energy absorbed per unit volume, or the toughness of the material.

A small percentage of the byssal thread stress–strain curves for each species differed dramatically from the characteristic shape of the curve for that species. In almost all cases, the discrepancy appeared to result from splitting and fraying of the thread prior to failure; we did not include the data from these samples in the analysis.

We analyzed the data using StatView 5.0 (SAS Institute, Cary, NC, USA). First, we conducted an ANOVA on the threads of each individual, followed by an ANOVA of all threads of each species, split by individual. Because no significant differences were detected, we then pooled the individuals within each species and ran an overall ANOVA, split by species. We performed *post-hoc* Scheffé tests to determine the specific differences detected by the ANOVA. We also ran a Kruskal–Wallis test (a non-parametric version of a standard ANOVA), as a normal distribution of the data could not be assumed. Finally, we produced a partial correlation matrix for each species to determine whether any two of the measured variables were significantly correlated when all other variables were held constant.

RESULTS

For all measured variables, ANOVA revealed no significant differences between threads of a given individual or between individuals of a given species; thus the threads for each species were pooled in the overall analysis.

As shown in Table 1, the overall ANOVA for diameter, which included mytilid species from a previous study (see Pearce and LaBarbera, 2009), revealed a clear division between semi-infaunal and epifaunal species: the threads of all epifaunal species were significantly thicker than those of all semi-infaunal species (Scheffé test: $P < 0.012$). Threads of epifaunal species were 2–4 times the diameter of threads of infaunal species. However, the threads of the epifaunal *C. mitis* were significantly thinner than those of one of the three other epifaunal species, *M. californianus* (Scheffé test: $P = 0.007$). While the shells of the mytilid species fell into a similar size range (60–70 mm on average), those of *C. mitis* were somewhat smaller and those of *A. rigida* were much larger.

‘True’ stress and strain were used to construct the stress–strain curves for all of the byssal thread samples. The curve of a representative byssal thread from each species is given in Fig. 1. Mytilid stress–strain curves from a previous study (Pearce and LaBarbera, 2009) have been included for comparison. The curve for *C. mitis* (green) exhibits a dramatically different shape from those of other threads examined to date – it has an early yield point and then a very long region of relatively uniform, low stiffness, finally stiffening slightly and breaking at an extremely high strain.

Strikingly, the *A. rigida* curve (Fig. 1, yellow) exhibits two distinct yield points. Thus *A. rigida* threads have a stress–strain curve similar to those of *M. modiolus* (Fig. 1, light blue), which display the same double-yield behavior (Fig. 2). *Atrina rigida* and *M. modiolus*, both semi-infaunal species, have threads that yield twice before failure, while the threads of all tested epifaunal species exhibit only a single distinct yield point.

In terms of byssal thread mechanical properties, *C. mitis* and *A. rigida* differed significantly from each other as well as from species within the Mytilidae. As Fig. 1 suggests, the threads of *C. mitis* were consistently weaker and less stiff than those of other species, often significantly so (Table 2). In addition, *C. mitis* threads yielded at a significantly lower stress than all other threads tested. However, despite their low strength and stiffness, *C. mitis* threads proved highly extensible, with an average final strain of 81% (Table 2). This extensibility was significantly greater than that of all other byssal threads tested, which ranged between 44% and 67%. Nevertheless, even with this higher strain to failure, *C. mitis* threads were significantly less tough than those of most mytilid species due to their low strength (Table 2).

The *A. rigida* threads were significantly weaker, in terms of both strength and toughness, than the majority of mytilid threads (Table 2). The threads of most species tested were significantly stiffer at the end of the test (paired *t*-test: $P < 0.0001$; paired sign test: $P < 0.0001$), but *A. rigida* and *G. demissa* threads did not exhibit a

Table 1. Byssal thread diameter and shell length

Species	Thread diameter (μm)	Range in shell length (mm)
<i>Geukensia demissa</i>	37.6 \pm 2.3 (32) ^A	62.2–76.9 [69.1 \pm 1.6] (11)
<i>Modiolus modiolus</i>	46.3 \pm 2.4 (28) ^A	49.2–72.3 [57.9 \pm 2.0] (12)
<i>Atrina rigida</i> *	54.2 \pm 3.3 (20) ^A	119, 131 (2)
<i>Ctenoides mitis</i> *	103.5 \pm 13.2 (30) ^B	43.3–59.3 [49.4 \pm 1.7] (10)
<i>Perna canaliculus</i>	129.7 \pm 8.2 (34) ^{B,C}	50.0–70.0 [62.3 \pm 2.7] (7)
<i>Mytilus edulis</i>	132.3 \pm 6.0 (55) ^{B,C}	58.6–88.4 [72.6 \pm 3.4] (10)
<i>Mytilus californianus</i>	149.6 \pm 6.6 (30) ^C	49.4–91.4 [70.0 \pm 6.1] (7)

Values given are means \pm s.e.m., followed by the sample size (N). Data for species marked with an asterisk are from this study. All other data are from our previous study (Pearce and LaBarbera, 2009). There were significant differences in thread thickness between species (ANOVA: $P < 0.0001$; Kruskal–Wallis: $P < 0.0001$). Values marked with the same superscript letter are not significantly different from one another (Scheffé test). Each of the semi-infaunal species – first three rows – had significantly thinner threads than each of the epifaunal species – last four rows (Scheffé test: $P < 0.0120$).

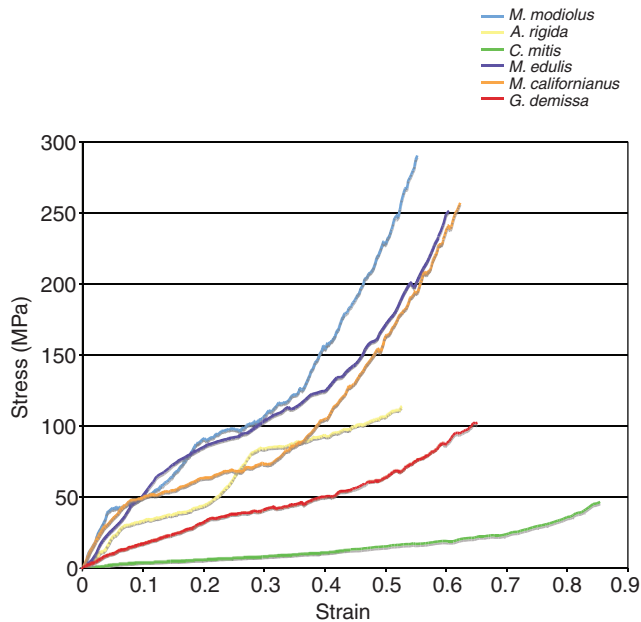


Fig. 1. Byssal thread stress–strain curves. A typical stress–strain curve was chosen for each species. Curves from a previous study have been included for comparison (Pearce and LaBarbera, 2009). Note that the *Atrina rigida* curve (yellow), like that of *Modiolus modiolus* (light blue), has two distinct yield points. The *Ctenoides mitis* curve (green) shows that these threads had extremely low strength and stiffness but were very extensible.

pronounced stiffening at higher strains. However, *A. rigida* threads were quite stiff at the outset, and had the highest average value for initial stiffness: 609 MPa (Table 2). Although they were stiff, the threads of *A. rigida* had a low extensibility. In stark contrast to the extremely stretchy threads of *C. mitis*, those of *A. rigida* had an average strain at failure of only 44%, significantly lower than that of all other threads tested (Table 2). Overall, the mechanical properties of the threads of *C. mitis* and *A. rigida* differed substantially from those of mytilid threads.

For all bivalve species examined to date, stronger threads tended to be tougher, and threads with a higher yield stress had a higher initial stiffness (Table 3). Whereas the significant correlations between properties of *C. mitis* threads followed patterns similar to those of mytilid threads, the *A. rigida* correlations seemed specifically to parallel those of *M. modiolus*. Like the byssal threads of *M. modiolus* but unlike those of all other species, the strength of *A. rigida* threads was not highly correlated with their failure stiffness (Table 3). Again like *M. modiolus*, tougher *A. rigida* byssal threads tended to exhibit a higher final stiffness, the opposite of the relationship found for the other species. Finally, initial and final stiffness for *A. rigida* and *M. modiolus* threads were not highly correlated, which contrasts with the results for *G. demissa* and *M. edulis* threads (Table 3). (For a complete list of property values for all individual threads tested in this study, see supplementary material Table S1.)

DISCUSSION

The correlation found here between life habit (epifaunal vs semi-epifaunal) and byssal thread diameter mirrors a similar relationship among mytilids [see accompanying paper (Pearce and LaBarbera, 2009)]. The association between semi-epifaunal life habits and small thread diameters found within the Mytilidae might have been due to the fact that tested mytilid species with similar life habits were closely

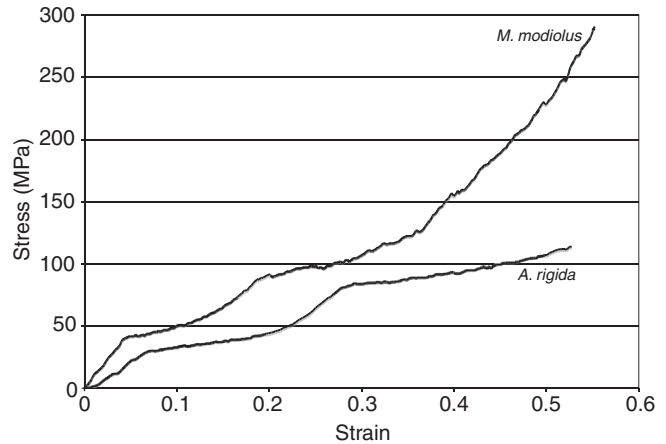


Fig. 2. Double-yield behavior. These curves illustrate the double-yield behavior of *A. rigida* and *M. modiolus* threads. Each curve has two distinct yield points, each represented by a relatively sudden drop in stiffness (the slope of the curve). Following each yield point, the thread becomes stiffer prior to either once again yielding or failing.

related to one another – although *Geukensia* is not a sister taxon of *Modiolus*, the two epifaunal mytilids tested are both in the genus *Mytilus* (Distel, 2000). However, the data on byssal thread diameter presented here for three different pteriomorph orders strengthens considerably the connection between life habit and byssal thread size. And although shell length (i.e. size) is likely involved in determining thread diameter within species (Brazee and Carrington, 2006), it is striking that threads produced by the *A. rigida* specimens, whose shells measured over 100 mm and were the largest in our study, were significantly thinner than those produced by the much smaller mytilids.

As previously observed among mytilids (Meadows and Shand, 1989), semi-epifaunal species seem to produce a very large number of thin threads, whereas epifaunal species produce a smaller number of thicker threads. One reason for this difference might be that having a larger number of thin threads is more effective in anchoring semi-epifaunal animals within a particulate substrate, as the threads can create an extensive network of individual attachments to small particles. The *M. modiolus* examined in a previous study tended to leave the glass plates to which we tried to confine them and bury themselves in the gravel, from which they were difficult to extricate without digging (Pearce and LaBarbera, 2009). For *Mytilus* species, on the other hand, which attach to rocks and other hard substrates, a smaller number of thick threads may provide a more reliable tether against wave action or predation (Bell and Gosline, 1996; Bell and Gosline, 1997; Carrington, 2002; Carrington and Gosline, 2004). The stalk-like byssus of some arcoids and pteroids may be an extreme form of this tendency to consolidate material into a smaller number of thicker threads (Oliver and Holmes, 2006; Tëmkin, 2006). *Ctenoides mitis* appears to represent a somewhat different case, as it only uses byssal threads for temporary attachment, and not for predator resistance; thus a set of weak but stretchy threads of intermediate thickness allows it to hang inside crevices, ready to drop the threads and swim away on disturbance.

The stress–strain curve of *A. rigida* threads exhibits two very clear yield points (Fig. 2), as seen previously for *M. modiolus* byssal threads (Brazee and Carrington, 2006). It would be interesting to re-examine existing molecular analyses of *M. modiolus* and *A. rigida* threads (Mascolo and Waite, 1986; Rzepecki et al., 1991) in light of this

Table 2. Byssal thread material properties

Species (N)	Yield stress (MPa)	Strength (MPa)	Initial stiffness (MPa)	Final stiffness (MPa)	Extensibility	Toughness (J m ⁻³)
<i>Atrina rigida</i> (13)	24.5±2.8 ^{A,B}	90.2±12.8 ^A	609.2±86.0 ^{A,B}	167.8±33.7 ^A	0.444±0.033 ^A	24.1±4.3 ^{A,B}
<i>Ctenoides mitis</i> (18)	5.2±0.7 ^C	55.1±06.0 ^A	101.6±18.4 ^C	210.0±30.3 ^A	0.805±0.031 ^B	15.9±2.0 ^B
<i>Geukensia demissa</i> (19)	23.9±4.2 ^B	140.8±18.7 ^{A,B}	324.7±60.8 ^{A,B,C}	319.1±45.2 ^A	0.637±0.018 ^C	43.3±5.6 ^{A,B,C}
<i>Modiolus modiolus</i> (20)	35.5±5.8 ^{A,B}	287.8±35.6 ^C	593.3±94.6 ^B	1039.6±129.0 ^B	0.571±0.024 ^C	67.4±8.5 ^C
<i>Mytilus californianus</i> (21)	33.0±2.9 ^{A,B}	215.3±25.3 ^{B,C}	432.3±45.5 ^{A,B}	810.0±93.9 ^B	0.640±0.016 ^C	51.7±5.9 ^{A,C}
<i>Mytilus edulis</i> (25)	44.4±6.6 ^A	216.9±18.8 ^{B,C}	328.6±30.8 ^{A,C}	784.4±62.7 ^B	0.669±0.017 ^C	56.9±6.3 ^C
Scheffe test, <i>P</i> -values	<0.0327	<0.0369	<0.0475	<0.0034	<0.0302	<0.0347

Values given are means ± s.e.m. Data for species in the last four rows are from our previous study (Pearce and LaBarbera, 2009). For each material property listed, the null hypothesis of similar values across species was robustly rejected (ANOVA: $P < 0.0001$; Kruskal–Wallis: $P < 0.0001$). In each column, values marked with the same superscript letter are not significantly different from one another (Scheffe test). Because the yield point was not obvious in all tests, only 12 *M. edulis*, 13 *M. modiolus* and 20 *M. californianus* data points were used in the analysis for yield stress.

unusual yield pattern, which seems to imply an underlying two-phase molecular structure. *Atrina rigida* and *M. modiolus* byssal threads have a great deal in common: they display an obvious double-yield behavior; they have a comparatively high initial stiffness and a comparatively low extensibility; and they share correlations not seen in the byssal threads of other species between stiffness at failure and other mechanical variables (Fig. 2, Table 2, Table 3). As *M. modiolus* and *A. rigida* are members of different orders within the Pteriomorphia (the Mytiloidea and Pterioidea) that are not sister taxa (Giribet and Wheeler, 2002; Matsumoto, 2003; Bieler and Mikkelsen, 2006), these commonalities suggest that their thread characteristics may be the product of convergent evolution. However, the threads of the only other semi-infaunal species tested, *G. demissa*, do not exhibit any of these characteristics. *Geukensia demissa* individuals often occur clumped together in marshy areas populated by sea grasses – the roots of the sea grasses, combined with the network of thin threads produced by the animals, may provide a strong attachment, mitigating any selection for stiffer threads or complex yield behavior (Stanley, 1970). In contrast, *A. rigida* and *M. modiolus* are often found living singly in the absence of sea grasses. To further examine the correlation between a semi-infaunal life habit and byssal thread characteristics, one could test the threads of other semi-infaunal mytilids and pinnids, e.g. *Modiolus americanus* Leach, which often lives in grass flats, or *Pinna nobilis* Linnaeus, which does not, to see whether they exhibit similar properties (Peterson and Heck, 2001).

Lucas and colleagues (Lucas et al., 1955) performed a tensile test on a single *P. nobilis* byssal thread submerged in (presumably distilled) water at 20°C and generated a stress–strain curve. They report ‘stress’ as force per linear density (grams per denier), a

variable commonly used in the textile literature which unfortunately confounds volumetric density and cross-sectional area. Thus, without knowing the volumetric density of the *P. nobilis* thread tested, it is impossible to calculate its breaking stress as defined in the engineering and biomechanics literature. (A similar problem applies to their reported value for strain rate.) Nonetheless, a comparison of strain values is possible: the *P. nobilis* thread broke at an ‘engineering’ strain of about 56%, a value close to the average ‘engineering’ extensibility of *A. rigida* threads, 57%; moreover, the yield strain of the *P. nobilis* thread was in the same range as that of *A. rigida* threads, although the former yielded at only a single point whereas the latter exhibited a second yield point at a higher strain. It would be unwise to place too much weight on this comparison, however, given that it is based on a single *P. nobilis* thread that was likely dried – and shipped from Milan to Manchester – before being re-hydrated and strained at an unknown rate.

As shown above, *C. mitis* threads have mechanical properties that differ dramatically from those of other species. Its threads are not strong, stiff or tough, but they are highly extensible. The ‘true’ strain at failure of these threads, 81%, corresponds to an ‘engineering’ strain of 126%, by far the highest ever recorded for distal or whole byssal threads (Bell and Gosline, 1996; Lucas et al., 2002; Brazeel and Carrington, 2006). These properties of *C. mitis* point to a possible trade-off in thread design. As with many engineered materials, it may be difficult to build a thread that is both very stiff and very extensible. This interpretation is supported by the observation that the stiffest threads are the least extensible (*A. rigida*, *M. modiolus*), whereas the highly extensible *C. mitis* threads have the lowest stiffness (Table 2). Assuming this trade-off,

Table 3. Selected coefficients from partial correlation matrices

Species (N)	Strength–toughness	Yield stress–initial stiffness	Strength–final stiffness	Toughness–final stiffness	Initial stiffness–final stiffness
<i>Atrina rigida</i> (13)	0.793	0.649	–0.068	0.311	0.054
<i>Ctenoides mitis</i> (18)	0.758	0.126	0.883	–	–
<i>Geukensia demissa</i> (19)	0.955	0.410	0.706	–0.551	0.514
<i>Modiolus modiolus</i> (13)	0.855	0.620	–0.159	0.549	0.091
<i>Mytilus californianus</i> (21)	0.982	0.579	0.756	–0.641	–
<i>Mytilus edulis</i> (12)	0.952	–	0.769	–0.603	0.563
<i>P</i> -values	<0.0001	<0.0001	<0.0025	<0.0004	<0.0446

Byssal thread strength and toughness were highly correlated ($R > 0.75$) for all species. Yield stress was well correlated with initial stiffness in most cases. The final stiffness of *A. rigida* and *M. modiolus* threads tended not to share the correlations seen in threads of other species (entries in bold). Non-significant correlations are not shown.

there are (at least) two possible hypotheses for the properties of *C. mitis* threads: (1) there has been no selection for costly strength/stiffness, and the high extensibility is a by-product; or (2) there has been selection for high extensibility, and the low strength/stiffness is a by-product. One explanation for (1) might be that high strength and stiffness are primarily important for resisting predator manipulation and wave action, which are perhaps not important factors for nestling, mobile *C. mitis*. On the other hand, a possible explanation for (2) is that, as with viscid spider silk, the highly extensible threads act as single-use shock absorbers, allowing *C. mitis* to absorb heavy currents or sudden shocks without abandoning a preferred crevice (Denny, 1976). Investigation of the thread properties of unrelated nestling bivalve species could provide evidence for or against (2). The ancestral condition for byssal thread properties is unfortunately unknown, as no one has studied the chemistry or mechanics of juvenile bivalve byssal threads.

Interestingly, the threads of *A. rigida* seem to share certain properties with those of each of the other two semi-infaunal species tested. Like those of *G. demissa*, its threads have a low yield stress, low strength and low toughness, but like those of *M. modiolus*, they have a high initial stiffness and a low extensibility (Table 2). Commonalities such as these are easy to explain away as being related to functional requirements: with a large number of threads and external support from the substrate, strength and toughness may be less important; and if the threads have very little give (high stiffness, low extensibility), that could stop predators from easily manipulating the animal. However, *post-hoc* explanations such as these do not solve the problem of why the three semi-infaunal species diverge in certain of their properties. This problem is impossible to fully address without research into the threads of other semi-infaunal mytilids and pinnids, as well as unrelated species with similar life habits.

As the data presented here demonstrate, pinnid and limid byssal threads have mechanical properties that often differ significantly from those of mytilid threads. Despite these differences, however, our data suggest a connection between the semi-infaunal life habit and certain thread properties, e.g. small diameter and double-yield behavior. A wider survey of bivalve byssal thread properties, both within and beyond the orders examined to date, would provide a wealth of information about connections between thread properties and evolutionary patterns within the Bivalvia. Moreover, with further work on byssal thread composition outside the Mytilidae, connections between microscopic molecular structures and macroscopic material properties might suggest new avenues for ongoing biomimetic research (Yu and Deming, 1998; Yamada et al., 2000; Tonegawa et al., 2004; Waite et al., 2005; Lee et al., 2006; Lee et al., 2007; Waite, 2008). Thus the comparative biomechanics of bivalve byssal threads has much to offer to both evolutionary biology and materials engineering.

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Table S1. Complete database of byssal thread properties

Species	Thread length (mm)	Thread diameter (mm)	Thread area (mm ²)	Maximum force (N)	Total displacement (mm)	Maximum engineering stress (MPa)	Maximum true stress (MPa)	Yield stress (MPa)	Initial stiffness (MPa)	Final stiffness (MPa)	Toughness (MJ m ⁻³)	Engineering failure strain	True failure strain	Yield strain
<i>Mytilus edulis</i>	5.95	123.27	0.01193	1.12923	4.84909	94.619	171.731		308.57	732.51	34.91	0.8150	0.5961	
<i>Mytilus edulis</i>	6.37	106.44	0.00890	1.36117	6.14978	152.973	300.657		485.75	1303.30	69.89	0.9654	0.6757	
<i>Mytilus edulis</i>	5.91	95.24	0.00712											
<i>Mytilus edulis</i>	3.99	114.36	0.01027	1.23440	5.22537	120.176	277.560		241.25	1242.45	78.02	1.3096	0.8371	
<i>Mytilus edulis</i>	2.97	119.55	0.01123	1.34394	4.11769	119.727	285.719		405.22	911.79	94.26	1.3864	0.8698	
<i>Mytilus edulis</i>	4.35	76.49	0.00460	0.97601	5.17023	212.399	464.848		861.21	1485.28	158.31	1.1886	0.7832	
<i>Mytilus edulis</i>	5.00	149.01	0.01744	1.71933	4.53773	98.591	188.067		307.07	624.54	46.53	0.9075	0.6458	
<i>Mytilus edulis</i>	4.31	146.27	0.01680											
<i>Mytilus edulis</i>	5.74	101.85	0.00815	1.26691	5.27240	155.501	298.334		231.10	948.29	71.41	0.9185	0.6516	
<i>Mytilus edulis</i>	13.00	221.85	0.03866											
<i>Mytilus edulis</i>	4.59	168.81	0.02238											
<i>Mytilus edulis</i>	7.54	109.90	0.00949	1.26169	7.12932	133.005	258.765		453.78	1201.72	56.76	0.9455	0.6655	
<i>Mytilus edulis</i>	5.51	129.46	0.01316	0.97097	4.69504	73.764	136.618		286.78	641.68	28.82	0.8521	0.6163	
<i>Mytilus edulis</i>	3.29	137.87	0.01493	1.26458	2.72134	84.706	154.771		319.45	600.46	35.51	0.8272	0.6028	
<i>Mytilus edulis</i>	2.43	170.30	0.02278											
<i>Mytilus edulis</i>	1.99	162.38	0.02071	1.41659	1.30066	68.405	113.115		231.46	577.57	23.21	0.6536	0.5030	
<i>Mytilus edulis</i>	2.93	126.73	0.01261	0.78030	1.96721	61.860	103.394		271.02	483.36	21.18	0.6714	0.5137	
<i>Mytilus edulis</i>	2.43	122.77	0.01184	1.36462	1.94775	115.275	207.673		341.66	834.55	45.67	0.8015	0.5886	
<i>Mytilus edulis</i>	7.05	132.02	0.01369	1.18339	6.81169	86.449	169.976	28.29	252.15	744.32	40.85	0.9662	0.6761	0.1161
<i>Mytilus edulis</i>	4.89	86.15	0.00583	0.95015	4.55899	163.001	314.968	68.65	560.19	1058.42	87.26	0.9323	0.6587	0.1231
<i>Mytilus edulis</i>	5.08	167.34	0.02199	1.01060	4.66764	45.950	88.171	20.92	150.94	336.84	24.09	0.9188	0.6517	0.1409
<i>Mytilus edulis</i>	3.44	106.93	0.00898	1.07627	4.07404	119.848	261.787	57.90	328.83	770.03	82.72	1.1843	0.7813	0.1771
<i>Mytilus edulis</i>	3.88	141.04	0.01562	1.26328	3.87312	80.859	161.574	30.26	204.81	597.35	41.80	0.9982	0.6923	0.1503
<i>Mytilus edulis</i>	4.30	153.62	0.01853											
<i>Mytilus edulis</i>	4.02	136.14	0.01456											
<i>Mytilus edulis</i>	3.31	136.61	0.01466											
<i>Mytilus edulis</i>	3.07	153.42	0.01849											
<i>Mytilus edulis</i>	2.86	78.13	0.00479	0.90012	2.78469	187.748	370.552	53.56	405.31	1111.43	96.81	0.9737	0.6799	0.1266
<i>Mytilus edulis</i>	3.16	127.28	0.01272											
<i>Mytilus edulis</i>	5.70	62.66	0.00308	0.36525	5.65701	118.446	235.998	44.22	394.88	897.39	61.20	0.9925	0.6894	0.1210
<i>Mytilus edulis</i>	3.95	60.40	0.00287	0.28216	3.87623	98.476	195.112	40.41	373.49	482.10	55.18	0.9813	0.6838	0.1267
<i>Mytilus edulis</i>	3.86	73.76	0.00427											
<i>Mytilus edulis</i>	3.58	67.69	0.00360	0.47135	3.52749	130.979	260.036	92.24	291.18	697.31	69.08	0.9853	0.6858	0.3076
<i>Mytilus edulis</i>	3.51	69.64	0.00381	0.39888	3.47887	104.721	208.513	60.37	154.41	614.77	52.44	0.9911	0.6887	0.3037
<i>Mytilus edulis</i>	5.03	168.82	0.02238	0.84694	4.61254	37.837	72.534	14.91	106.47	244.04	18.52	0.9170	0.6508	0.1439
<i>Mytilus edulis</i>	4.74	109.41	0.00940											
<i>Mytilus edulis</i>	5.42	109.07	0.00934	0.61135	4.73575	65.432	122.604	21.55	246.86	469.40	28.85	0.8738	0.6279	0.1098
<i>Mytilus edulis</i>	15.68	176.24	0.02439											
<i>Mytilus edulis</i>	10.48	118.30	0.01099											
<i>Mytilus edulis</i>	12.74	201.91	0.03202											
<i>Mytilus edulis</i>	12.32	211.72	0.03521											
<i>Mytilus edulis</i>	11.36	223.29	0.03916											
<i>Mytilus edulis</i>	9.84	202.97	0.03236											
<i>Mytilus edulis</i>	11.64	216.39	0.03678											
<i>Mytilus edulis</i>	9.68	132.92	0.01388											
<i>Mytilus edulis</i>	9.65	114.94	0.01038											
<i>Mytilus edulis</i>	8.90	129.22	0.01311											
<i>Mytilus edulis</i>	7.58	138.62	0.01509											
<i>Mytilus edulis</i>	10.09	139.18	0.01521											
<i>Mytilus edulis</i>	9.83	127.73	0.01281											
<i>Mytilus edulis</i>	7.58	169.90	0.02267											
<i>Mytilus edulis</i>	9.84	224.77	0.03968											
<i>Mytilus edulis</i>	8.74	57.15	0.00257											
<i>Mytilus edulis</i>	8.15	73.44	0.00424											
<i>Mytilus edulis</i>	9.38	95.85	0.00722											
<i>Mytilus californianus</i>	11.03	162.87	0.02083	1.51435	8.53079	72.687	128.904	38.67	512.59	672.20	31.96	0.7734	0.5729	0.0948
<i>Mytilus californianus</i>	12.89	172.03	0.02324	2.32569	14.24610	100.059	210.644	30.47	427.59	800.96	50.47	1.1052	0.7444	0.0962
<i>Mytilus californianus</i>	8.03	165.84	0.02160											
<i>Mytilus californianus</i>	8.53	159.02	0.01986	1.42642	6.76300	71.821	128.765	30.04	486.45	592.14	29.12	0.7928	0.5838	0.0913
<i>Mytilus californianus</i>	17.20	142.77	0.01601	1.67643	21.03828	104.718	232.805	24.91	378.30	1086.22	52.82	1.2232	0.7989	0.0970
<i>Mytilus californianus</i>	7.94	85.89	0.00579	1.51519	9.32712	261.512	568.710	37.63	408.12	2135.38	129.46	1.1747	0.7769	0.0980
<i>Mytilus californianus</i>	12.15	155.83	0.01907											
<i>Mytilus californianus</i>	9.57	87.46	0.00601											
<i>Mytilus californianus</i>	8.17	115.63	0.01050	1.16941	8.50809	111.362	227.333		118.41	929.87	46.60	1.0414	0.7136	
<i>Mytilus californianus</i>	14.62	130.25	0.01332	1.36402	11.21990	102.371	180.933	30.73	540.69	663.40	41.76	0.7674	0.5695	0.0752
<i>Mytilus californianus</i>	15.00	131.93	0.01367	1.88715	12.97468	138.048	257.457	29.12	810.09	883.07	63.00	0.8650	0.6232	0.0372
<i>Mytilus californianus</i>	12.11	151.53	0.01803	1.37417	8.74170	76.200	131.205	31.80	410.73	409.54	31.69	0.7219	0.5434	0.0938
<i>Mytilus californianus</i>	12.19	128.05	0.01288	2.07095	11.31396	160.813	310.069	54.00	814.48	1185.47	74.78	0.9281	0.6566	0.0861
<i>Mytilus californianus</i>	9.96	135.99	0.01452	1.42830	7.60157	98.336	173.388	46.54	581.01	834.48	43.73	0.7632	0.5671	0.0908
<i>Mytilus californianus</i>	13.85	131.37	0.01355											
<i>Mytilus californianus</i>	14.84	244.57	0.04698											
<i>Mytilus californianus</i>	10.36	157.92	0.01959											
<i>Mytilus californianus</i>	10.06	122.80	0.01184	1.26453	9.17638	106.769	204.159	37.17	497.27	636.54	50.88	0.9122	0.6482	0.0901
<i>Mytilus californianus</i>	17.40	215.35	0.03642											
<i>Mytilus californianus</i>	11.98	170.06	0.02271	1.84328	11.15336	81.152	156.704	22.16	158.11	612.99	37.99	0.9310	0.6580	0.1412
<i>Mytilus californianus</i>	9.46	122.59	0.01180	1.24228	8.21469	105.249	196.644	24.66	381.29	818.15	49.43	0.8684	0.6251	0.0707
<i>Mytilus californianus</i>	10.44	171.26	0.02304											
<i>Mytilus californianus</i>	9.87	144.72	0.01645	2.16596	9.67913	131.675	260.803	30.80	351.75	1010.34	61.90	0.9807	0.6834	0.1007
<i>Mytilus californianus</i>	15.90	147.03	0.01698											
<i>Mytilus californianus</i>	10.99	183.83	0.02654	0.50302	8.10432	18.952	32.928	5.21	69.18	138.85	7.94	0.7374	0.5524	0.0737
<i>Mytilus californianus</i>	9.40	226.49	0.04029	2.46425	7.79949	61.164	111.914	24.50	244.54	303.00	29.46	0.8297	0.6042	0.1071
<i>Mytilus californianus</i>	13.35	100.26	0.00789	1.48839	13.39975	188.526	377.755	43.05	548.48	1361.02	92.08	1.0037	0.6950	0.0929
<i>Mytilus californianus</i>	9.95	132.38	0.01376	0.56842	7.92276	41.298	74.182	13.15	116.60	242.94	18.47	0.7963	0.5857	0.1017
<i>Mytilus californianus</i>	9.16	150.64	0.01782	3.01471	8.49207	169.151	325.968	50.75	589.82	927.76	84.34	0.9271	0.6560	0.0887
<i>Mytilus californianus</i>	9.48	141.58	0.01574	2.04114	7.30638	129.652	229.576	54.76	632.99	765.60	57.49	0.7707	0.5714	0.1037
<i>Modiolus modiolus</i>	4.95	57.67	0.00261	0.26603	3.43978	101.845	172.618		328.14	1024.56	40.05	0.6949	0.5276	
<i>Modiolus modiolus</i>	4.91	60.40	0.00287	0.23352	2.55916	81.501	123.980	24.75	516.51	522.77	24.90	0.5212	0.4195	0.0502
<i>Modiolus modiolus</i>	2.79	40.84	0.00131	0.25411	1.99964	193.979	333.008	37.47	704.09	1105.60	76.00	0.7167	0.5404	0.0504
<i>Modiolus modiolus</i>	2.25</													

<i>Geukensia demissa</i>	5.38	58.28	0.00267												
<i>Geukensia demissa</i>	4.34	50.01	0.00196												
<i>Geukensia demissa</i>	5.02	30.04	0.00071												
<i>Geukensia demissa</i>	6.79	46.28	0.00168	0.13816	6.87994	82.132	165.352	23.41	384.91	317.78	56.56	1.0132	0.6997	0.0661	
<i>Geukensia demissa</i>	3.50	42.72	0.00143	0.13497	4.10649	94.163	204.643	18.53	229.20	376.36	65.61	1.1733	0.7762	0.0741	
<i>Geukensia demissa</i>	6.88	55.40	0.00241	0.13980	7.66804	57.994	122.632	19.13	201.50	261.36	39.96	1.1145	0.7488	0.1150	
<i>Atrina rigida</i>	7.33	27.60	0.00060												
<i>Atrina rigida</i>	11.51	69.97	0.00385												
<i>Atrina rigida</i>	7.13	76.30	0.00457	0.10470	3.61183	22.899	34.499	11.15	225.94	39.81	8.35	0.5066	0.4098	0.0534	
<i>Atrina rigida</i>	9.65	46.54	0.00170	0.11420	6.70146	67.134	113.755	29.64	505.31	217.15	34.30	0.6945	0.5274	0.0674	
<i>Atrina rigida</i>	6.49	43.57	0.00149	0.14252	3.06528	95.591	140.739	38.54	1048.31	70.04	30.01	0.4723	0.3868	0.0582	
<i>Atrina rigida</i>	9.98	49.37	0.00191	0.08328	3.74969	43.502	59.847	27.04	721.84	139.35	13.94	0.3757	0.3190	0.0434	
<i>Atrina rigida</i>	7.56	86.92	0.00593												
<i>Atrina rigida</i>	7.02	54.14	0.00230	0.10256	3.81781	44.550	68.779	23.81	620.98	111.07	18.94	0.5438	0.4343	0.0478	
<i>Atrina rigida</i>	14.42	39.78	0.00124	0.12650	5.83862	101.782	142.993	42.33	1168.09	379.98	27.78	0.4049	0.3400	0.0450	
<i>Atrina rigida</i>	7.89	68.82	0.00372	0.08961	3.20962	24.091	33.890	10.61	108.92	50.28	5.67	0.4068	0.3413	0.0875	
<i>Atrina rigida</i>	8.06	51.49	0.00208	0.12846	4.17625	61.691	93.656	23.44	549.82	147.01	22.45	0.5181	0.4175	0.0410	
<i>Atrina rigida</i>	6.93	57.66	0.00261												
<i>Atrina rigida</i>	7.84	40.11	0.00126												
<i>Atrina rigida</i>	8.36	70.58	0.00391												
<i>Atrina rigida</i>	12.30	49.18	0.00190	0.08747	3.94593	46.046	60.817	22.79	713.64	89.14	10.72	0.3208	0.2782	0.0389	
<i>Atrina rigida</i>	7.95	64.24	0.00324	0.06502	6.25867	20.061	35.853	9.11	182.66	65.44	12.20	0.7873	0.5807	0.0682	
<i>Atrina rigida</i>	8.91	49.67	0.00194												
<i>Atrina rigida</i>	9.47	47.53	0.00177	0.11327	6.52627	63.841	107.837	26.68	608.94	228.75	32.92	0.6892	0.5242	0.0509	
<i>Atrina rigida</i>	10.18	38.69	0.00118	0.07210	6.86849	61.326	102.703	24.28	707.30	227.26	31.91	0.6747	0.5156	0.0381	
<i>Atrina rigida</i>	15.30	52.76	0.00219	0.19236	15.59884	87.985	177.689	29.12	758.39	415.74	64.23	1.0195	0.7029	0.0455	

Material properties of the byssal threads of selected bivalve molluscs. Empty cells represent missing values. 'Engineering' stress and strain (σ_E , ϵ_E) are defined as $\sigma_E = F/A_0$ =force/unit initial area, $\epsilon_E = \Delta L/L_0$ =change in length/initial length; 'true' stress and strain (σ_T , ϵ_T) are defined respectively as $\sigma_T = \sigma_E \exp(\epsilon_T)$ (assuming constant volume, i.e. a Poisson's ratio of 0.5) and $\epsilon_T = \ln(L/L_0)$. Yield stress and strain were defined as a sharp drop in stiffness at a characteristic stress and strain level; thread stiffness was determined both for the initial loading of the thread and at thread failure. The area under the stress-strain curve (the energy absorbed per unit volume, or the toughness of the material) was determined by fitting a polynomial to the curve and integrating over the total strain. A Microsoft® Excel® version of this file is available from the authors upon request.