

2004

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Mechanical design of mussel byssus: Load cycle and strain rate dependence

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Abstract: The ability to produce a strong byssal attachment is one key to the competitive dominance of mussels on many rocky shores. The byssus is composed of numerous extracellular collagenous threads, which in turn can be divided into proximal and distal regions that are distinct in ultrastructure and chemical composition. Our current understanding of the mechanical design of mussel byssus is largely based on quasi-static testing, where a fiber is slowly extended to failure. Mussels in nature, however, inhabit a dynamic environment where repetitive loads can be applied on short time scales. This study evaluates the mechanical properties of the threads of *Mytilus californianus* subjected to repeated subcritical loads and a range of strain rates. A subset of these mechanical tests was also performed on the threads of three other mytilid species. Results indicate that subcritical loading alters the mechanical properties of a thread in a manner that is dependent on the extension applied, and that thread stiffness and damping increase with increasing strain rate. Overall, this study provides insight into the mechanical design of a byssus that is subjected to dynamic loading.

Key words: *Mytilus*, byssal thread, modulus, strength, resilience

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Mussels often dominate hard surfaces in temperate aquatic habitats, in part due to their ability to produce a strong attachment in the form of a byssus. Mussel byssus is composed of numerous byssal threads, each formed within a groove in the mussel foot by a process resembling polymer injection-molding (Waite 1992). The threads tether the mussel by providing the link between the substratum (via the adhesive plaque) and the stem/root system that is embedded in the byssal gland of the foot (Brown 1952; Fig. 1). The threads of mytilid mussels are extracellular collagenous fibers that can be divided into two distinct regions: (1) the corrugated *proximal* region, and (2) the smoother, narrower *distal* region that represents approximately two-thirds the total thread length (Bell and Gosline 1996).

The distinct ultrastructure and molecular composition of the two regions have been the focus of numerous studies (recently reviewed by Waite *et al.* 1998). The corrugated sheath of the proximal region covers loosely packed coiled fibrils, while the distal region contains dense bundles of filaments. Three collagenous proteins have been identified in the thread, each a natural block copolymer with a central collagen domain flanked by different domains: preCol P with elastin-like flanking

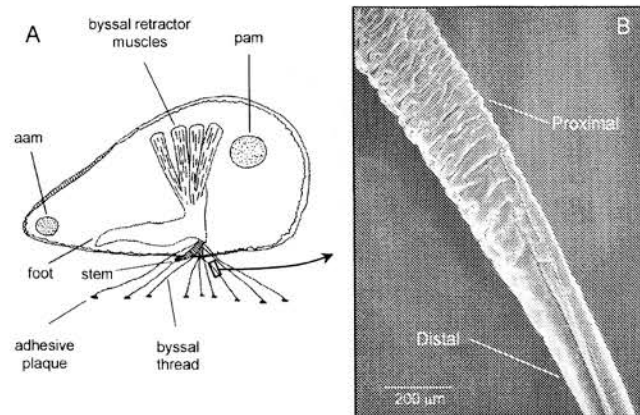


Figure 1. A. Anatomy of mussel byssus and musculature, adapted from Waite (1992). Approximate mussel shell length is 4 cm. Abbreviations: am, anterior adductor muscle; pam, posterior adductor muscle. B. Scanning electron micrograph of a portion of a *Mytilus californianus* thread, showing the transition from the corrugated proximal region to the smooth distal region.

From the symposium "Frontiers in Functional Morphology" presented at the World Congress of Malacology, held 19-25 August 2001 in Vienna, Austria, and supported by the American Malacological Society and the National Science Foundation Ecological and Evolutionary Physiology Program (IBN-0090902).

domains; preCol D with silk-like flanking domains; and preCol NG with glycine-rich, cell wall-like domains. PreCol P and preCol D predominate in the proximal and distal regions, respectively, while preCol NG is distributed evenly throughout the thread.

Given these disparities in composition and structure, it is not surprising that the two regions have been shown to differ in mechanical properties as well. Bell and Gosline (1996) extended earlier biomechanical studies (Allen *et al.* 1976,

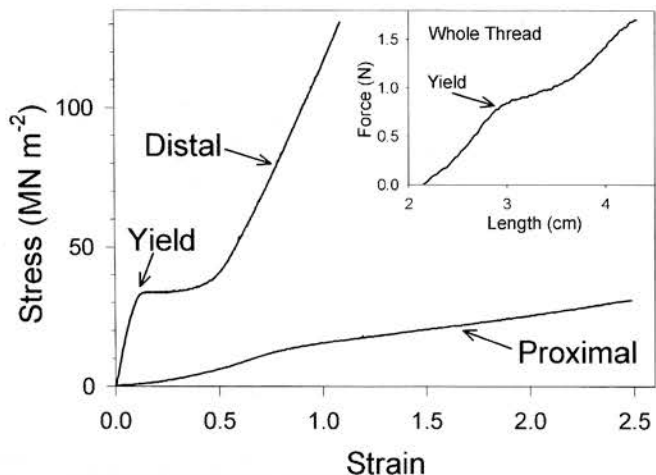


Figure 2. Representative tensile tests of two isolated regions and a whole thread (inset) of *Mytilus californianus*, after Bell and Gosline (1996). Note yield behavior of distal region is reflected in whole thread test. Extension rate = 10 mm min⁻¹.

Smeathers and Vincent 1979, Price 1981) in detailing the low stiffness, low strength, and high extensibility of the proximal region in comparison to the distal region in three mytilids (*e.g.*, Fig. 2).

Additionally, the distal region undergoes a distinct yield at approximately 20% extension, and then stiffens again before failure. The yield in the distal region plays the functionally important role of providing the extensibility needed to distribute an applied load over multiple threads, thereby increasing the strength of the entire byssus.

One limitation of these mechanical studies is that they involved quasi-static testing, in which threads were loaded to failure at relatively slow extension rates (5-25 mm min⁻¹, which corresponds to strain rates of 0.5-2.5 min⁻¹ for a 10 mm sample). Wave-swept mussels, however, are likely exposed to more rapid, repeated loading regimes (applied over less than one second, Denny *et al.* 1998, Gaylord 1999, 2000). An interest in the dynamic mechanical properties of byssal threads has developed recently (Waite *et al.* 1998,

Vaccaro and Waite 2001, Sun *et al.* 2001, Carrington 2002). These pioneering studies indicate that portions of mussel byssus exhibit the unusual properties of self-healing and strain-stiffening and may therefore provide insight into the design of novel polymers.

The purpose of this study is to provide a more detailed view of the dynamic mechanical behavior of byssal threads. By exposing whole threads and isolated thread regions to repeated subcritical loads and a range of strain rates, we demonstrate that subcritical loading alters the mechanical properties of byssal threads in a manner that is dependent on the amount of deformation that was applied. Furthermore, the overall stiffness and energy dissipation of byssal threads increases with increasing strain rate.

METHODS

Mytilus californianus Conrad, 1837 was the primary test species for this study, and all mechanical tests described here were performed on threads from *M. californianus*. A subset of these mechanical tests was also performed on other mytilids: *Mytilus trossulus* Gould, 1850, *Mytilus galloprovincialis* Lamarck, 1819, and *Mytilus edulis* Linnaeus, 1758. With the exception of *M. edulis*, all animals were collected from Barkley Sound (48.8°N; 125.1°W) on the west coast of Vancouver Island, British Columbia, Canada. *M. edulis* was collected from Bass Rock in Rhode Island Sound (41.4°N, 71.5°W). Animals were maintained at 10-15°C in gently recirculating seawater for up to four months. Individual threads were carefully removed from their attachment points (the stem of the byssus and the substrate) and maintained unstretched in seawater until testing. Only one thread per individual was tested, either whole or only in the distal or proximal region. Each end of the sample was glued between two balsa wood tabs with cyanoacrylate and clamped within the testing apparatus. All mechanical tests were conducted in seawater at 15 ± 1°C.

Quasi-static testing

A tensometer was used to perform quasi-static testing, in which the force required to extend slowly a sample to a given length was recorded. An Instron-1122 tensometer was used for all tests, with modifications described by Bell and Gosline (1996), except for tests with *Mytilus edulis*, where an Instron-5565 equipped with a computer interface was used. Both tensometers were capable of a maximum extension rate of 1000 mm min⁻¹. When applicable, force measurements were converted to stress (σ , in N m⁻²) by dividing by the cross-sectional area of the specimen. This area was assumed to be circular

and was calculated from a sample diameter measured with an ocular micrometer ($\pm 1 \mu\text{m}$). Measurements of specimen length (l) were converted to strain (ϵ) using the formula $\epsilon = (l-l_0)/l_0$, where l_0 is the initial unstressed length of the specimen. A strain value of 1 is equivalent to 100% extension, or a doubling of specimen length. Initial modulus (E_i) describes the stiffness of a material and is calculated as the slope (σ/ϵ) of the initial linear portion of a stress-strain curve.

Cyclical loading

A preliminary exploration of cyclical loading was first performed on whole threads from *Mytilus californianus*, in which a specimen was extended 5 mm min^{-1} to a subcritical length, returned to its initial length, and then extended to failure. A thread was cycled to one of two extensions: 11% (below the yield point) and 44% (well into the yield region). Data from the first cycle were used to calculate sample resilience, R , as the area under the return curve expressed as a percentage of the area under the extension curve. Resilience is a measure of elastic efficiency, or the percentage of elastic strain energy stored during deformation that is recovered in elastic recoil. Resilience is 100% for a perfectly elastic material, but is much lower for a material that dissipates strain energy through molecular friction (Gosline *et al.* 2002). Additionally, the percent change in initial modulus (0-11% extension) from the first to the second cycle was calculated.

More extensive mechanical tests were performed on whole threads cycled to 11% extension to evaluate differences among species and among stages of thread maturation (or "tanning"). First, laboratory produced threads of *Mytilus californianus*, *Mytilus trossulus*, and *Mytilus galloprovincialis* were tested, with sample sizes of 7, 12, and 3, respectively. All threads were 1-6 days old and were golden yellow in appearance. Analysis of variance was used to evaluate the effect of species on the change in initial modulus from the first to second load cycle. Second, whole threads of *M. californianus* at different stages of maturation were tested: milky white (< 24 hours old), golden yellow (1-6 days old), and dark brown (harvested in the field, age unknown). Sample size was 4, 7, and 12, respectively. Analysis of variance was used to evaluate the effect of thread maturation on the change in initial modulus from the first to second load cycle.

Cyclical loading was also performed on isolated distal and proximal regions of threads of *Mytilus californianus*. Distal regions were isolated from four separate animals and subjected to repeated cycles to four extensions: 8%, 16%, 35%, and 65%. Note that the first two of these extensions are below the yield point, the third is within the yield region, and the last is beyond the yield region. Resilience was calculated for the first cycle of each extension level.

Based on the results of these preliminary tests, the

mechanical behavior of the distal region was explored in more detail using a time delay between extension cycles. Specifically, distal regions of the threads of *Mytilus californianus* were subjected to two extension cycles (either 35% or 65%), then left unstressed in 15°C seawater for 10 min, 30 min, 1 h, 16 h, 6 days, or 27 days. After the time delay, the two extension cycles were repeated. Three replicate distal samples were tested for each time delay, thus sample size was 18 for each of the two extensions. This protocol was also used for distal portions of the threads of *Mytilus edulis*, but only 35% extension cycles were performed and the 27-day treatment was omitted. Recovery of molecular structure in the distal region was calculated as the area enclosed by the force-extension loop after time delay expressed as a percentage of the area enclosed by the initial loop. Time values were log-transformed, and analysis of variance was used to evaluate (1) the effect of log-time and extension (35% vs. 65%) on the recovery of samples of *M. californianus* and (2) the effect of log-time and species (*M. californianus* vs. *M. edulis*) on the recovery of distal samples cycled to 35% extension (Systat version 10, Chicago, IL). Cyclical loading tests of proximal regions were less extensive overall; 7 specimens of *M. californianus* were cycled repeatedly to approximately 60% extension.

Strain rate dependence

Two methods were used to investigate the influence of strain rate on the mechanical properties of byssal threads from *Mytilus californianus*. The first method, performed only on paired samples from the same distal region, used the quasi-static tensometer (described above) at extension rates of 10 and 1000 mm min^{-1} . This method, while informative, was unable to achieve the extremes in extension rate that wave-exposed mussels are likely exposed to in nature ($>> 1 \text{ cm s}^{-1}$, Denny *et al.* 1998) due to limitations of the tensometer.

The second method, dynamic testing, applied more rapid extensions to isolated proximal and distal regions, following the procedure of Lillie and Gosline (1990). Distal and proximal samples isolated from the same thread of *Mytilus californianus* were prepared for dynamic testing by subjecting the thread portions to twenty load cycles in the tensometer at an extension rate of 5 mm min^{-1} . Extensions were 50% and .5% for the proximal and distal regions, respectively, corresponding to loads of 0.1 to 0.2 N, and had the effect of stabilizing the mechanical behavior of the samples. Each sample was then mounted in the dynamic test apparatus and placed under a small, static load (0.02-0.05 N, below the yield point of a whole thread). Small amplitude, sinusoidal deformations were then applied to the samples at a range of frequencies (0-5 Hz, followed by 0-200 Hz). Spectral analysis of the resulting stress and strain waveforms provided two

material properties for each frequency: (1) the dynamic modulus, E^* (in $N\ m^{-2}$), which is the ratio of the amplitudes of the stress and strain waveforms, and (2) δ , which is the phase shift between the two waveforms. The phase shift is generally reported as $\tan \delta$, and is an index of energy dissipation, or damping, of a material. Dynamic resilience can be calculated from these data using the formula: $R = e^{-2\pi \tan \delta}$ (Gosline *et al.* 2002). This equation reflects the full, sinusoidal deformation applied to the sample, but is not comparable to the resilience measured in quasi-static tests, because the latter most closely approximates a half cycle (a fiber cannot be compressed). Thus an alternative equation was used to calculate dynamic resilience per half cycle: $R = e^{-\pi \tan \delta}$.

RESULTS

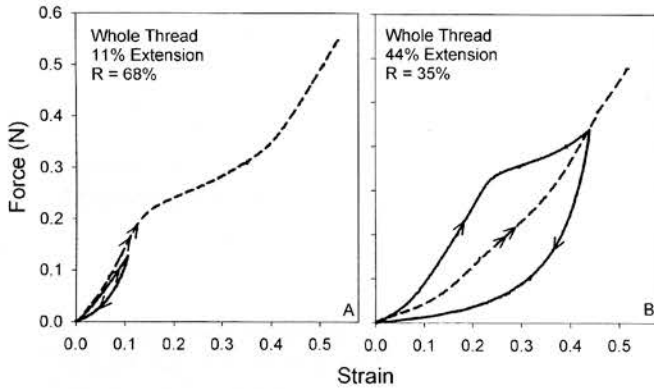


Figure 3. A single cycle of subcritical loading of whole threads of *Mytilus californianus* (solid line) followed by loading to failure (dashed line). A. Initial load cycle is below the yield strain (11% extension). B. Initial load cycle is beyond the yield strain (44% extension). Arrows indicate direction of loading; double arrows denote extension after initial cycle. Extension rate = 5 mm min⁻¹.

Cyclical loading

The mechanical behavior of whole threads depended on the extension to which they were cycled. The thread from *Mytilus californianus* shown in Fig. 3A was highly resilient (68%) when cycled to an extension below its yield point. When then loaded to failure, initial stiffness increased 22%, indicating that more force was required to achieve 11% extension. In contrast, the thread loaded beyond the yield point (44% extension, Fig. 3B), was much less resilient (35%) and a considerable amount of strain energy was dissipated in the cycle. When subsequently loaded to failure, the thread decreased in stiffness by 54% (measured over 0-11 % extension) and lacked a yield region.

Table 1. Change in initial modulus (stiffness) in whole threads of three *Mytilus* species cycled to 11% extension. Extension rate = 5 mm min⁻¹. SE = Standard error; N = sample size.

Species	Age	% change in initial modulus			
		Appearance	Mean	SE	N
<i>M. californianus</i>	1 – 6 days	Golden yellow	5.8	2.3	7
<i>M. trossulus</i>	1 – 6 days	Golden yellow	17.0	3.6	12
<i>M. galloprovincialis</i>	1 – 6 days	Golden yellow	17.9	5.0	3
<i>M. californianus</i>	< 24 hours	Milky white	14.1	2.1	4
<i>M. californianus</i>	Unknown (field-collected)	Dark brown	6.3	2.0	12

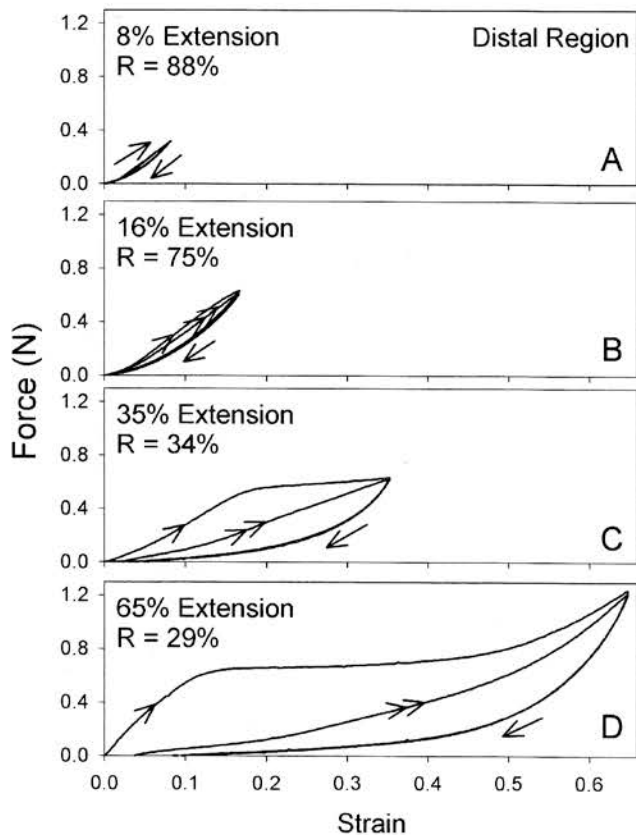


Figure 4. Cyclic loading of distal portions of byssal threads of *Mytilus californianus*, ranging from 8 to 65% extension (A-D, respectively). Arrows indicate direction of loading; double arrows denote second cycle extension. Resilience is calculated for first cycle only. Different threads were used for each extension, thus the first cycles do not overlap precisely. Extension rate = 5 mm min⁻¹ for A and B; 10 mm min⁻¹ for C and D.

The general trend of strain stiffening was observed in all threads cycled to 11% extension. The degree of strain stiffening in whole threads was indistinguishable among the three species tested (Table 1, golden yellow threads; $F = 2.91$, $P = 0.08$), and among the different stages of maturation (Table 1, *Mytilus californianus*; $F = 2.73$, $P = 0.09$). Note, however, that the statistical power of these analyses was low (0.31 and 0.34, respectively), due to sample size limitations.

Isolated portions of the distal regions of byssal threads of *M. californianus* also exhibited mechanical behavior that depended on the extension to which they were cycled. The distal region was stiff and highly resilient (88%) when cycled to a low extension (8%, Fig. 4A), and all subsequent cycles were indistinguishable from the first. When cycled to increasing extensions (16%-65%, Fig. 4B-D), the resilience of the first cycle decreased markedly (from 88% to 29%). Furthermore, the loading portion of the second cycle was less stiff than the first cycle, and this disparity increased with increasing cycle extension. The unloading (return) portions of the two cycles were identical for all extensions, and the third and all subsequent cycles were indistinguishable from the second cycles (data not shown).

The area enclosed by each force-extension loop represents the strain energy lost during deformation due to molecular friction. In previously unstressed, stiff threads cycled beyond their yield point, considerable energy was dissipated in the first cycle, but not in the second cycle (Fig. 5A). That is, the area enclosed by the second loop is only 38% of that enclosed by the first loop. Over time, however, the distal region began to increase in stiffness and recover the energy dissipating behavior of the first cycle. For example, when left unstressed for 30 minutes and then cycled twice, the area enclosed by the first force-extension loop at $t = 30$ min was 68% of the first cycle at $t = 0$. The subsequent cycle then reverted to a loop similar to the second cycle at $t = 0$.

The area enclosed by a force-extension loop after a time delay expressed as a percentage of the area enclosed by the initial loop provides an index of "recovery" of molecular structure in the distal region. In threads from *Mytilus californianus*, recovery increased as a logarithmic function of time ($F = 464.7$, $P < 0.001$) and depended on the extension that was applied ($F = 24.9$, $P < 0.001$; Fig. 5B). The interaction between log time and extension was not significant ($F = 0.8$, $P = 0.37$), thus threads cycled to 65% extension recovered at the same rate, but took longer to achieve a given level of recovery because they exhibited a greater initial loss of stiffness. Only 50 - 60% recovery was achieved in 30 minutes, and full recovery required several weeks. The general behaviors of the load cycles were similar for distal portions of threads of *Mytilus*

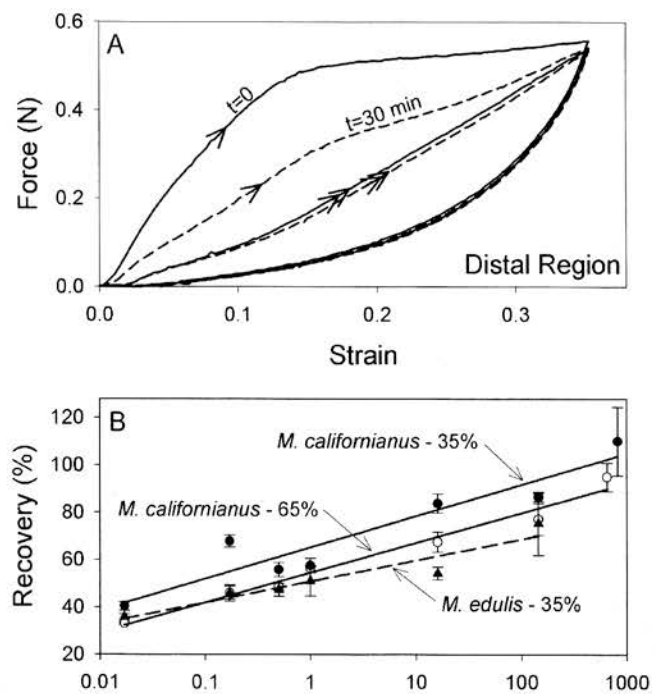


Figure 5. Cyclic loading of the distal portion of a byssal thread with a time delay. A. Representative test of a thread from *Mytilus californianus* loaded to 35% extension. Two cycles were conducted at $t = 0$ (solid lines), followed by two more cycles after a 30 minute delay (dashed lines). The area enclosed by each force-extension loop represents the strain energy lost due to deformation. Adapted from Bell (unpublished data) in Waite et al. (1998). B. Recovery of energy dissipation in threads of *M. californianus* (loaded to 35% and 65% extension, solid and open circles, respectively) and *Mytilus edulis* (loaded to 35% extension only, triangles) as a function of time. Recovery was calculated as the energy dissipated at time t divided by the energy dissipated at time $t = 0$ (see text for details). Symbols are mean values \pm SE, $n = 3$. Extension = 10 mm min^{-1} .

edulis, but the rate of recovery at 35% extension was reduced in comparison to those of *M. californianus* (species \times log time interaction, $F = 8.5$, $P < 0.01$; Fig. 5B).

Isolated portions of the proximal regions of the byssal threads of *Mytilus californianus* were highly variable in mechanical behavior when cycled. Many thread samples increased in stiffness when cycled; an extreme example of this behavior is shown in Fig. 6. This sample, taken from an unstressed thread produced in the laboratory, initially increased in stiffness and resilience with each successive cycle. The material stabilized after approximately 15 cycles, with an overall 80% increase in stiffness and 60% increase in resilience compared to the first cycle. Cyclical loading of the other samples exhibited only modest stiffening, or none at all (data not shown).

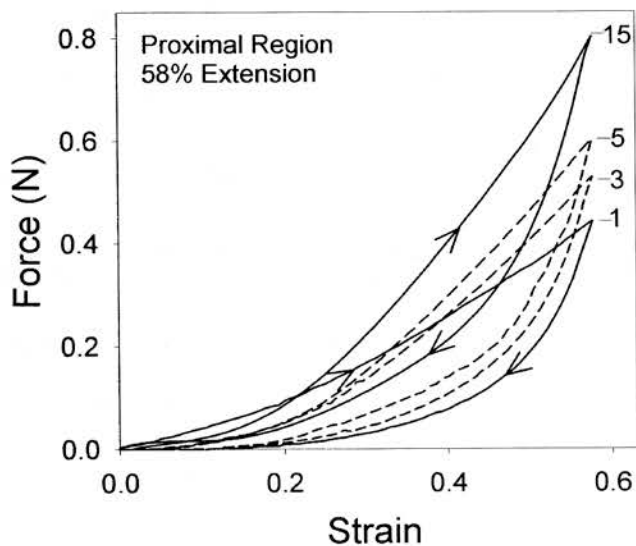


Figure 6. Cyclic loading of proximal region of a byssal thread. This thread from *Mytilus californianus* was cycled fifteen times to 58% extension at a rate of 5 mm min^{-1} (only cycles 1, 3, 5, and 15 are shown for clarity). Resiliences for cycle 1 and 15 are 42% and 67%, respectively.

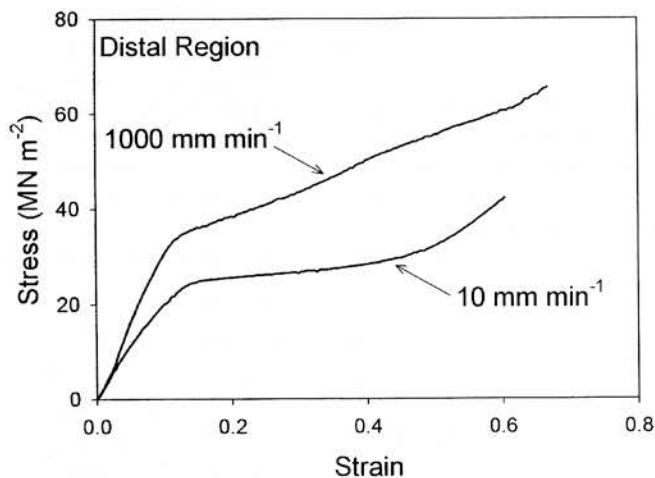


Figure 7. Mechanical testing of the distal region of a byssal thread at two extension rates, 10 mm min^{-1} and 1000 mm min^{-1} . Samples were taken from the same thread of *Mytilus californianus*. Both samples failed at one of the grips, thus these tests underestimate the ultimate properties of the samples.

Strain rate dependence

The mechanical behavior of byssal threads also depended on the rate at which they were extended. When a distal region was divided into two samples, each tested at a different extension rate, the sample strained at the higher rate exhibited increased stiffness and yield stress. For the thread shown in Fig. 7, the sample tested at 1000 mm min^{-1} was 60% stiffer and yielded at a 40% higher stress than the sample tested at the slower extension rate. The yield strain remained unchanged, and the yield "plateau" was less distinct at the higher extension rate. Unfortunately, grip failures were very common with this protocol and it was not possible to evaluate the effect of strain rate on ultimate properties of the distal region.

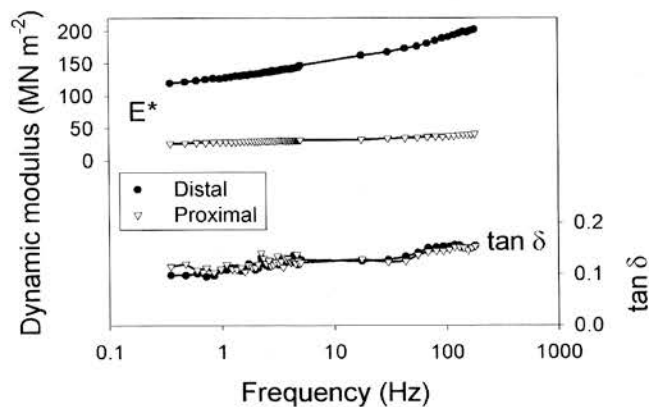


Figure 8. Dynamic mechanical properties of proximal and distal regions from the same byssal thread of *Mytilus californianus*. Static load was 0.022 N and 0.046 N for proximal and distal regions, respectively. Data were smoothed with a five-point running average; only every fifth point is plotted.

The dynamic moduli of isolated regions of byssal threads increased with increasing frequency (Fig. 8). Over three decades of frequency, the dynamic modulus, E^* , ranged from 27 to 41 MN m^{-2} in the proximal region, and from 120 to 202 MN m^{-2} in the distal region. $\tan \delta$ also increased with test frequency, ranging from 0.10 to 0.15 for both thread regions, and dynamic, half-cycle resilience ranged correspondingly from 97% to 62%.

DISCUSSION

This study demonstrates that the mechanical behavior of mussel byssus described in quasi-static studies (e.g., Smeathers and Vincent 1979, Bell and Gosline 1996) is not

fixed, but instead depends on the loading history of the thread. In *Mytilus californianus*, whole threads cycled below the yield point were highly resilient and increased slightly in stiffness when loaded once again. This strain-stiffening behavior did not depend on the maturation of the thread, and has also been observed in *Mytilus trossulus* and *Mytilus galloprovincialis* (this study) and *Mytilus edulis* (Carrington 2002). In contrast, threads cycled beyond the yield point had much lower resiliency and were dramatically less stiff when reloaded. These unusual behaviors are due to the load cycle dependence of the two components of the threads, the proximal and distal regions.

At low extensions, the strain-stiffening behavior of whole threads was solely due to the properties of the proximal region, where stiffness and resilience can increase dramatically upon cycling. The distal region was very stable at these extensions, and because the proximal region is the smaller portion of the thread (20-40%), the strain-stiffening effect in whole threads was less dramatic. Cycled proximal regions eventually stabilized and began to exhibit more characteristic stress-softening behavior (deforming slightly with each successive cycle). We observed that the number of cycles required to achieve this state was highly variable among "virgin" threads that were recently produced in the laboratory (1-6 days old). Sun *et al.* (2001) explored the molecular basis of irreversible strain stiffening in the proximal region of byssal threads of *M. galloprovincialis*, demonstrating that it can be achieved by aeration and prevented by oxygen depletion in the absence of mechanical loading. While this clever observation provides invaluable insight into the biomolecular structure of this material, it is difficult to imagine how it might apply to mussels that typically inhabit well-stirred and aerated environments in nature. Indeed, we observed strain stiffening behavior in both threads that were young (milky white) and well-aged (tanned) in the field. Thus the process and functional importance of strain stiffening in naturally occurring byssal threads remains unclear.

The loss of resiliency and stiffness in whole threads cycled beyond the yield point was due to the properties of the distal region, which exhibits stable, highly resilient cycles when loaded below the yield point. When loaded beyond the yield point, the distal region deformed and dissipated energy via molecular friction. In the short term (minutes), the region remained deformed and subsequent cycles exhibited low stiffness and only modest energy dissipation. In the long term (days), the deformation was reversible and the distal region recovered to a stiff, energy-dissipating fiber. This ability to "self-heal" (*sensu* Vaccaro and Waite 2001) was dependent on the amount of deformation applied, with greater deformations requiring a longer recovery.

For a given extension, self-healing was more rapid in threads from *Mytilus californianus* in comparison to *Mytilus edulis* (this study) and *Mytilus galloprovincialis* (Vaccaro and Waite 2001). These results extend the observations of Bell and Gosline (1996, 1997) that threads of *M. californianus* outperform those of "edulis-like" species (*M. edulis*, *M. galloprovincialis*, and *M. trossulus*; McDonald and Koehn, 1988) in stiffness, extensibility, and thickness. The inferior threads of "edulis-like" species are not necessarily maladaptive, since these mussels typically inhabit calmer shores and have "weedy" life histories (rapid growth, early reproduction) that may compensate for a weaker mechanical design (Koehl 1999). Threads of *M. californianus* and *M. edulis* differ in amino acid composition (Mascolo and Waite 1986), but the biomolecular basis for the superiority of *M. californianus* threads (particularly in the distal region) is at this point unknown.

Mussels living on rocky shores are subjected to dynamic loading by waves arriving approximately every ten seconds (Denny 1988). Because waves often travel in "sets," extreme forces on mussels are likely generated in rapid succession, on a time scale of seconds to minutes. If a single wave is large enough to load a thread beyond its yield point, the thread is able to dissipate much of that energy via deformation in the distal region. But full recovery from this deformation is quite a slow process, and the thread will certainly face the next wave with compromised stiffness. The remaining threads would then follow the same process in subsequent waves. Although the strength of each individual thread remains unaltered, such a reduction in thread stiffness reduces the overall attachment strength of a mussel (~20%; Bell and Gosline 1996). Thus it appears that mussels should avoid loading individual threads beyond their yield point, and Bell and Gosline (1996) suggest that this is exactly what they do: the estimated stress per individual thread for a typical wave falls well below the yield stress for *Mytilus californianus*.

The discussion above is based on mechanical tests performed at slow strain rates that are not characteristic of the rapid loading to which wave-swept mussels are subjected in nature (Denny *et al.* 1998, Gaylord 1999, 2000). Distal regions of byssal threads of *Mytilus californianus* are stiffer and yield at a higher force when strain rate is increased. Similar observations have been made for the distal regions of threads from *Mytilus galloprovincialis* (Vaccaro and Waite 2001). Dynamic tests indicated that both the proximal and distal regions of the threads of *M. californianus* increased in stiffness and became less resilient with increasing test frequency, suggesting that whole threads do as well. According to the model of Bell and Gosline (1996), increased stiffness and yield force in individual threads would enhance the strength of the entire byssus. Thus mussels exposed to rapid loading may have increased

attachment strength in comparison to mussels that are loaded slowly.

This study furthers our view of the mechanical design of mussel byssus by considering the dynamic environment in which mussels live. While the dynamic mechanical properties of byssal threads have by no means been characterized completely, unique properties have been identified and provide an enhanced framework for biomolecular studies aimed at improving the design of man-made fibers (e.g., Vaccaro and Waite 2001, Sun *et al.* 2001), and for ecomechanical studies that explore the hydrodynamic loading of flexible, wave-swept organisms (e.g., Denny *et al.* 1998).

ACKNOWLEDGMENTS

We thank Mario Kasapi and Margo Lillie for helpful discussions and technical guidance. Frank Gibbons and Joe Mello also provided technical assistance, and John Hazard provided computer expertise at a critical point in this study. This work was supported by a Killam Postdoctoral Fellowship, an Eloise Gerry Fellowship of the SDE/Graduate Women in Science, Bamfield Marine Station, the University of Rhode Island, NSERC (grant no. 86934 to J.M.G.) and NSF (grants 9711893 and 0082605 to E.C.).*

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Accepted: 29 April 2003

* This publication was written in celebration of our collective 100th birthday, December 14, 2003.