

The Ecomechanics of Mussel Attachment: From Molecules to Ecosystems¹

EMILY CARRINGTON²

Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881

SYNOPSIS. One aspect of the physiological ecology of intertidal organisms is their mechanical design, which can be explored at many hierarchical levels, from molecules to ecosystems. Mechanical structures, as with any other physiological feature, require energy to construct and maintain, are subject to manufacturing and evolutionary constraints, and influence ecological performance. This contribution focuses on the ecomechanics of mussel attachment, which contributes to the competitive dominance of mussels on many wave-swept shores. Examples are presented to illustrate the hierarchical nature of mussel attachment, how levels of the hierarchy are interrelated, and where gaps in our knowledge remain. For example, water motion generates forces that mechanically deform byssal threads, but may also enhance the rate at which threads subsequently restore their original toughness. Furthermore, the ability of mussels to sense and respond to changes in their flow environment by producing a stronger attachment may be subject to physiological constraints, which in turn may have important consequences for the ecological response of mussels to shifts in wave climate. Thus an integrative approach to the study of byssal attachment is needed to fully understand this important aspect of the physiological ecology of mussels on rocky intertidal shores.

INTRODUCTION

Physiological ecology is the study of how organisms interact with their physical environment, and how such interactions influence their distribution and abundance. In the case of wave-swept rocky intertidal habitats, the physical environment can be quite demanding. When the tide is high, flowing water can generate large hydrodynamic forces on attached organisms (via the transfer of the water's momentum). When the tide is low, terrestrial (aerial) conditions can heat and desiccate organisms beyond their tolerances. Thus intertidal physiological ecology is intimately dependent on the transfer of momentum, heat, and mass (*e.g.*, water, oxygen, nitrogen) between organisms and their environment.

In general terms, the transfer of momentum, heat, or mass is driven by a concentration gradient at a rate inversely proportional to the resistance to transfer. Thus the three transfer processes are governed by analogous physical principles, and for this reason, they are often addressed simultaneously in engineering texts. It has been the tradition in biology, however, to segregate these processes into different disciplines. Heat and mass transfer processes are featured in standard plant and animal physiology texts that detail organismal temperature, water relations, and gas exchange. Organismal processes involving momentum transfer, on the other hand, are treated separately in functional morphology and biomechanics texts (*e.g.*, Denny, 1988; Vogel, 1994; Niklas, 1992). Wainwright and Reilly (1994) have argued compellingly that physiology *includes* functional morphology and biomechanics, and thus a complete view of the physiological

ecology of any organism must take all three transfer processes into consideration. This latter point certainly applies to rocky intertidal organisms and is discussed in considerable detail by Denny and Wethey (2001).

The overwhelming majority of the contributions in this volume address temperature and/or water relations. This is likely due to the many important technological and philosophical advances that have been made in these areas in recent years, but may also reflect the common view that the numerous ecomechanical studies on intertidal organisms do not fall within the envelope of physiological ecology. In an effort to overcome this bias, this contribution focuses on mechanical aspects of the physiological ecology of intertidal organisms. Specifically, I highlight the mechanics of attachment of the marine mussel from the molecular to ecosystem level. The examples presented here are primarily for the blue mussel *Mytilus edulis* and were selected to illustrate the many hierarchical levels that influence mussel attachment, and by no means represent an exhaustive review of the mussel attachment literature.

The mussel byssus

Mussels often dominate primary space on rocky intertidal shores, largely due to their ability to maintain a strong byssus (Fig. 1). This attachment structure is commonly referred to as the "beard" because it is fibrous, proteinaceous, and extracellular. The byssus is secreted by the mussel foot, and is composed of numerous byssal threads, each connecting proximally to a common stem that is rooted within the byssus gland of the foot and ultimately connects to the byssus retractor muscles (Brown, 1952). The threads tether the mussel by radiating from the stem to the substrate, where each thread terminates in an adhesive plaque. Byssal thread formation differs from that of other animal protein fibers (*e.g.*, keratin, silk) in that threads are produced within a groove in the foot by a process

¹ From the Symposium *Physiological Ecology of Rocky Intertidal Organisms: From Molecules to Ecosystems* presented at the Annual Meeting of the Society for Comparative and Integrative Biology, 2–7 January 2002, at Anaheim, California.

² Formerly E. C. Bell; e-mail: carrington@uri.edu

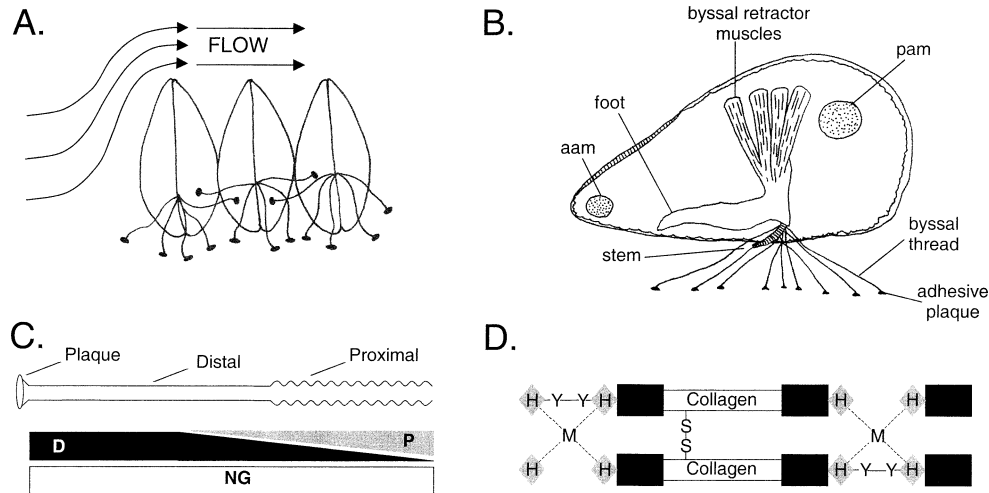


FIG. 1. The hierarchical structure of mussel byssus. A. Cross-section of mussel bed in flow. While a typical byssus contains 30–50 threads (Bell and Gosline, 1997), only a few per individual are represented here. B. Cross-section of a mussel, illustrating byssus and major musculature (adapted from Waite, 1992). Anterior and posterior adductor muscles are designated *aam* and *pam*, respectively. C. A single *M. edulis* thread, with corresponding distribution of three preCols (P, D, and NG; after Waite *et al.*, 1998). D. Generalized model of PreCol, indicating possible cross-links between subunits (after Vaccaro and Waite, 2001). Flanking domains (solid boxes) have characteristic sequence for each PreCol; H and Y represent histidine- and DOPA-rich domains, respectively. Cross-links involve metal chelates (M), disulfides (S-S), and oxidized DOPA residues.

resembling polymer injection-molding (Waite, 1992). This allows the mussel to form two morphologically distinct parts in each thread: a *proximal region* that is relatively thick and corrugated, and a *distal region* that is thin and smooth. The proximal region typically extends just beyond the shell margin; the distal region is entirely external. Laboratory studies have shown that the metabolic cost of byssal thread production can be substantial, up to 8% of a mussel’s monthly energy expenditure (Hawkins and Bayne, 1985). It is the strength of the byssus, relative to the forces imposed on it, that determines whether a mussel will remain attached to its substrate. For this reason, attachment is an important component of the physiological ecology of mussels.

MUSSEL BYSSUS: FROM MOLECULES TO ECOSYSTEMS

The molecules of mussel byssus

Much of our current understanding of the molecular structure of mussel byssus comes from the work of J. H. Waite and colleagues (see Waite *et al.*, 1998 for a recent overview). Collagen is the dominant protein in byssal threads; the proximal region can be considered a composite material, with collagen-like fibrils reinforcing a soft protein matrix, while the distal region contains densely-packed bundles of collagenous fibers. To date, three collagenous thread proteins have been characterized: PreCol P and PreCol D are distributed in complementary gradients along the thread and are most abundant in the proximal and distal regions, respectively, while PreCol NG is evenly distributed throughout the thread (Fig. 1). The preCol molecules share a common block copolymer design, where a central collagen domain is flanked at each end by a specific structural domain, which then terminates with his-

tidine and DOPA-rich domains. The flanking domain of each preCol has a characteristic sequence, which resembles elastin (PreCol P), silk (PreCol D), or cell wall protein (PreCol NG). While the process of preCol assembly during thread formation is not known, Vaccaro and Waite (2001) suggest that a variety of intermolecular bridges (*e.g.*, metal chelate, diDOPA, and disulfide) may be involved.

There is recent evidence that the molecular architecture of mussel byssus may be influenced by environmental conditions in a variety of ways. For example, water flow enhances the formation of DiDOPA crosslinks in byssal plaques (McDowell *et al.*, 1999) and threads (Sun *et al.*, 2001). Furthermore, mussels placed on differing attachment surfaces vary the expression of adhesive plaque proteins (Florioli *et al.*, 2000). These studies suggest that not only habitat characteristics, but also a mussel’s response to them, can influence byssus structure at the molecular level.

Threads in tension

Given the differences in morphology and molecular composition of the proximal and distal regions, it is not surprising that they differ in mechanical properties as well. Tensile testing of the threads of a variety of species has shown that the distal region is not only stiffer, stronger, and less extensible than the proximal region, but also undergoes a distinctive yield before it breaks (Fig. 2; see Bell and Gosline, 1996 and references within). When the tensile behavior of a whole thread is considered, mechanical failure typically occurs in the adhesive plaque or proximal region, but only after the distal region yields (Fig. 3). Thus a byssal thread can be considered “elastic” in that it extends considerably before it breaks. The combination

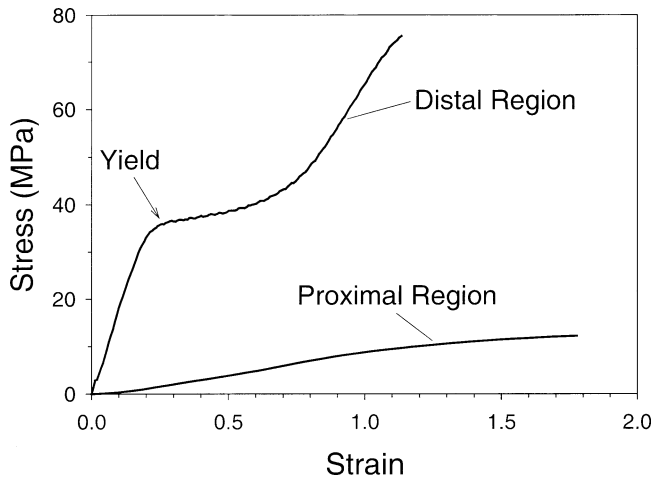


FIG. 2. Tensile tests of two regions isolated from *M. edulis* byssal threads, following methods of Bell and Gosline (1996). Initial length of proximal and distal sample was 5.8 and 3.6 mm, respectively. Tests were performed in 15°C seawater at an extension rate of 10 mm min⁻¹.

of high extensibility and high strength make byssal threads “tough” (able to absorb considerable strain energy before failure), with values that are comparable to Kevlar (Gosline *et al.*, 2002).

Another definition of elasticity is reversible deformation (Gosline *et al.*, 2002), and in this sense byssal threads are elastic in some instances, but not others. For example, threads loaded to modest extensions (<20%) exhibit tight, repeatable load cycles characteristic of a resilient (elastic) material (Fig. 3; Carrington and Gosline, 2003). When loaded to higher extensions (>20%, into the yield region and beyond), threads exhibit an open load cycle that is characteristic of a non-elastic, energy dissipating fiber. Upon subsequent loading, the thread is clearly deformed in that it is less stiff and tough (Fig. 3). Interestingly, threads are capable of recovering from this “irreversible” deformation over time (Waite *et al.*, 1998; Carrington and Gosline, 2003). At the molecular level, this recovery process likely involves alterations in the linkages between the preCol subunits (Vaccaro and Waite, 2001). Sun *et al.* (2001) have also shown that the stiffness of the proximal region is enhanced by agitation in water (using an orbital shaker), and that oxidative stress probably increases protein crosslinks. Thus the mechanical behavior of byssal threads not only depends on the nature of the applied load (magnitude, frequency, duration, etc.), but also on the chemical environment that surrounds the threads. Further investigation is needed to clarify the relationship between molecular structure and mechanical function of byssal threads.

The byssus as a structure

The mechanical behavior of byssal threads is therefore complex, and it can be somewhat perplexing as to what function many of these unusual properties serve. For example, if failure generally occurs in the

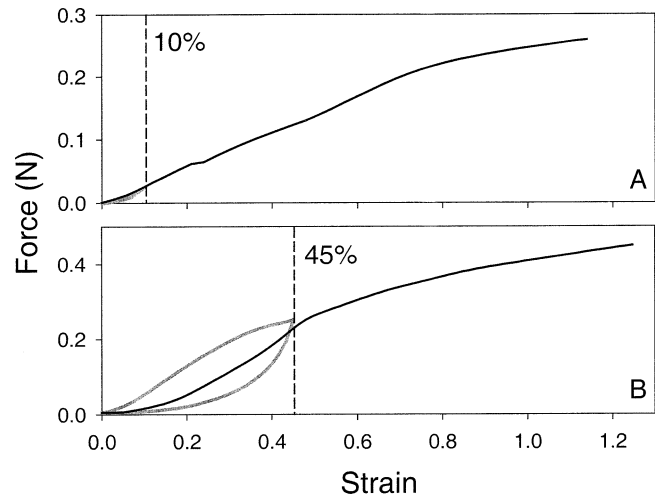


FIG. 3. Tensile tests of whole *M. edulis* threads, with one precycle (subcritical extension loop) followed by extension to failure. A. Pre-cycle to 10% extension, initial length = 5.6 mm. B. Pre-cycle to 45% extension, initial length = 10.4 mm. Tests were performed in 15°C seawater at an extension rate of 10 mm min⁻¹.

proximal region or the adhesive plaque, why is the distal region so strong? Bell and Gosline (1996) have shown that the distal regions of most mytilids are grossly overdesigned in terms of strength. They argue, however, that the most important mechanical property of the distal region is perhaps not its high strength, but its ability to yield (extend) at a specific force. The utility of this extensibility is only apparent when the role of each thread in an entire byssus is considered. Because mussels can be loaded in a variety of directions (Bell and Gosline, 1997), the overall load initially may not be evenly distributed among the numerous threads in a byssus. The yield of the distal region provides the extension needed to realign and recruit new threads to share the load, which has the effect of increasing the overall attachment strength of the mussel. In this manner, the mechanical function of an individual byssal thread is clear only when it is placed in the context of the higher-level structure in which it operates.

Forces on individuals

The absolute strength of mussel byssus, however, is of little concern to ecologists evaluating whether a byssus is “strong enough” to keep a mussel attached to its substrate. Instead, it is the strength of the byssus *relative* to the forces imposed on it that matters; if a mussel experiences a force that exceeds its byssal strength, it will be dislodged. The byssus can be loaded by internal sources (the contraction of the byssus retractor muscles), or from external forces on the shell (*e.g.*, flow, predators, neighboring mussels), which are then transferred to the byssus via the retractor muscles. Of these potential sources of byssal loading, the hydrodynamic forces generated by flowing water are likely the greatest, and most poorly understood, in wave-swept habitats. This is not only due to the dif-

faculty in characterizing complex surf-zone flows (*e.g.*, Bell and Denny, 1994; Gaylord, 1999, 2000), but also because the forces experienced by mussels in a given flow have not been characterized, despite much theoretical conjecture (Denny, 1987; Bell and Gosline, 1997; Denny *et al.*, 1998). Note that the importance of accelerational forces on surf-zone organisms, as proposed Denny *et al.* (1985), has recently been questioned by Gaylord (2000) and is not presented here.

The model of hydrodynamic force generation on mussels with perhaps the best experimental evidence is that of Denny (1987), where a pressure differential develops between the top and bottom of each mussel as flow skims over the top of an aggregation. This has the potential of generating lift on a mussel in a direction perpendicular to the substrate, and Denny has proposed that lift can be substantial enough to dislodge individuals, forming gaps in a mussel bed. This mechanism of force generation would not apply to solitary mussels because the requisite pressure differential would not develop. Solitary mussels, however, directly intercept and reroute flow and thus would be subjected to drag acting parallel to the substrate. Because aggregated mussels typically assume a posture that minimizes the area exposed to flow (reducing lift, Fig. 1a), Bell and Gosline (1997) argue that flow forces are most severe for solitary mussels. Their observation that solitary mussels produce more byssal threads (effecting increased attachment strength) than bed mussels supports this view. Mussels in hummocks, which often form in densely packed mussel beds, project into flow and likely experience a combination of lift and drag that is more severe than either of the two scenarios discussed above.

A third model of flow forces on mussels is that of Denny *et al.* (1998), where the influence of byssus flexibility on the dynamics of force generation is specifically addressed. While their mathematical model only crudely approximates real-world mussels (a solitary mussel with uniform byssal threads is subjected to a generic flow bore), Denny *et al.* (1998) raise the important point that flexibility allows the mussel to briefly accelerate with flow before it is "jerked" to halt by its tether. This dynamic, inertial loading can exceed stationary loading (lift or drag) by a factor of five under some circumstances. While no direct measurements of the forces encountered by mussels are currently available to support any of these models, it is interesting to consider that hydrodynamic loading of the byssus may depend on its flexibility, which in turn depends on the mechanical properties of the byssus. In this manner, the dynamic mechanical behavior of byssus and hydrodynamic force generation on mussels are intimately linked.

Attachment in populations

Numerous studies have demonstrated that mussel attachment strength is not fixed, but instead varies considerably between and within populations. For example, attachment strength increases with wave exposure

between sites (Witman and Suchanek, 1984) and between habitats within a site (tidepool *versus* emergent rock, Hunt and Scheibling, 2001). Furthermore, mussels sheltered within a bed are weakly attached in comparison to solitary mussels or those on the fringe of a bed (Witman and Suchanek, 1984; Bell and Gosline, 1997), indicating that attachment strength depends on position as well. Much of this variation likely reflects the ability of a mussel to sense and respond to its flow environment by adjusting attachment strength via thread production (Seed and Suchanek, 1992; Bell and Gosline, 1997; Carrington, 2002).

Attachment strength also depends on mussel size, increasing nearly linearly with shell area exposed to flow (Denny, 1987; Bell and Gosline, 1997; Hunt and Scheibling, 2001). The primary source of this variation is not the number of threads present in the byssus, but rather, their thickness. In a morphometric analysis of two mytilid species, Bell and Gosline (1997) show that byssal thread diameter, which is determined by the size of the groove in the mussel foot, increases approximately with the square root of shell area. Consequently, the load-bearing area of the byssus (the sum of the cross-sectional areas of each byssal thread) increases linearly with shell area, and byssus strength largely keeps pace with hydrodynamic loading (as determined by shell area exposed to flow) during ontogeny.

Flow environment and mussel size alone by no means account for all of the observed variation in attachment strength in mussel populations. Hunt and Scheibling (2001) note that attachment strength does not always increase linearly with shell area, and that the effect of habitat on attachment strength depends on mussel size. Other factors influencing mussel attachment that warrant attention include variation in thread strength (due to biodegradation or other environmental influences on molecular crosslinking), microhabitat heterogeneity, substrate quality, and mussel mobility.

Additionally, the ecomechanics of multilayered mussel beds has not been explored fully. Byssal threads cannot exceed the length of the foot (where they are formed), so thread length is limited to ~60% the length of the shell in *M. edulis*. Mussels in the top layers have difficulty accessing primary substrate and must instead attach byssal threads to neighboring shells. Food-limitation in mussels at the bottom of multilayered beds may lead to reduced thread production, thereby weakening the attachment of the entire matrix to primary substrate. In this manner, mussel attachment strength may depend on population density.

Community influences

While mussels often dominate primary space on rocky shores, they also provide refuge and habitat for many organisms living on and amongst their shells (Suchanek, 1985). Epizoans can increase drag on a mussel by effectively increasing the area projected into flow (Witman and Suchanek, 1984). In the case where a mussel is overgrown by a kelp, the increased drag is sufficient to increase the mussel's risk of dislodg-

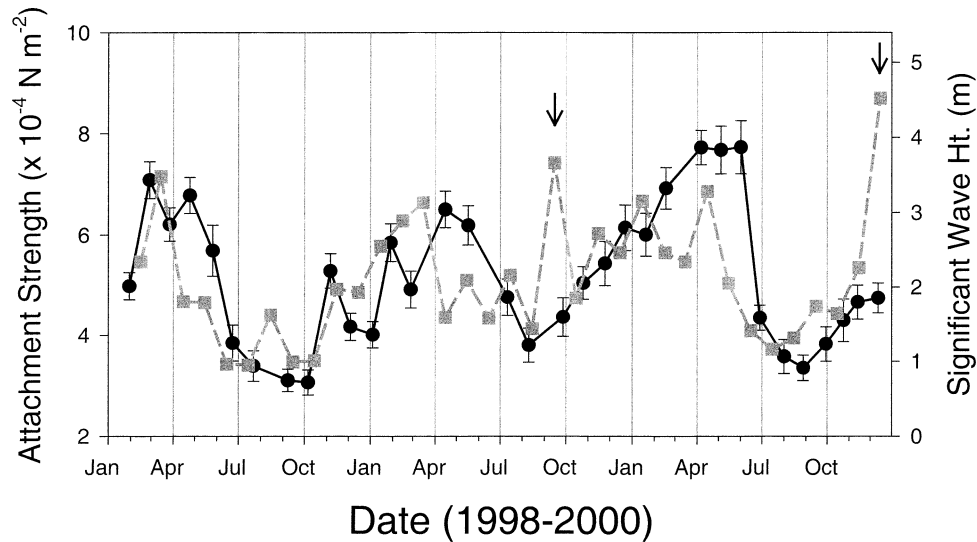


FIG. 4. Seasonal fluctuations in mussel attachment strength and wave climate, adapted from Carrington (2002). Mean attachment strength (black circles) of *M. edulis* at Bass Rock, RI. Symbols represent mean \pm SE of 50 samples. Attachment strength was calculated as dislodgment force divided by shell projected area. Monthly maximum daily mean significant wave height (squared) recorded at station BUZM3 in Buzzard's Bay, Massachusetts. Vertical reference lines approximately demarcate seasons, and arrows indicate periods of increased dislodgment risk. See Carrington (2002) for details.

ment. Witman (1987) has shown that kelp overgrowth (and the subsequent increase in storm-generated dislodgment) prevents the mussel *Modiolus modiolus* from dominating space in shallow subtidal habitats.

It is also important to consider that the byssus serves functions other than resisting the hydrodynamic forces generated by breaking waves. One example is provided by Leonard *et al.* (1999), where mussels on estuarine shores increase thread production in the presence of crab predators. This inducible response increases the mussel's attachment strength and thereby reduces the likelihood that it will be preyed upon. Because crab foraging activity is greatest at low flow sites, where their maneuverability is not hindered by hydrodynamic forces, mussel attachment is stronger at low flow sites than at moderate flow (crab-free) sites. This example of increased flow having an indirect negative effect on mussel attachment illustrates how community composition can blur the responses of mussels to flow alone.

Geographic and ecosystem variation

The attachment strength of a mussel population can vary temporally as well, generally decreasing in summer and increasing in winter, and is strongly correlated with seasonal fluctuations in wave climate (Price, 1982; Hunt and Scheibling, 2001; Carrington, 2002). While this appears to be yet another manifestation of a mussel's ability to sense and respond to its flow environment (similar to the way in which mussels respond to spatial variation in flow, as discussed above), it is important to note that mussels are not always precise in their response. For example, Carrington (2002) has shown that *M. edulis* on Rhode Island shores are slow to build up attachment strength following sum-

mer, perhaps due to energetic constraints on thread production during the reproductive season (Fig. 4). Consequently, the mussels are particularly susceptible to large dislodgment events at the onset of storm season (September–December); waves of equivalent magnitude arriving later in the storm season (January–May) pose less of a dislodgment risk because attachment strength has steadily increased.

A different scenario emerges from the study of Price (1982) on the coast of South Wales. Attachment strength in this *M. edulis* population also fluctuates seasonally, but peak attachment instead precedes the onset of storm season by 1–2 mo, then steadily declines to a minimum in April. Thus mussels in Wales are well prepared for storms arriving early in the season (October–December), but the risk of dislodgment increases as the storm season progresses. In particular, mussels are most susceptible to dislodgment at the tail end of the storm season (February–March).

Together, the studies of Carrington and Price indicate that there are windows of time where mussels are particularly at risk of dislodgment, due to the combined effects of reduced attachment strength and increased storm activity. Furthermore, the timing of increased dislodgment risk differs between the two studies because the temporal fluctuations in attachment strength are out of phase by approximately four months. Further study is required to determine why these populations differ in the timing of dislodgment risk and the extent to which windows of increased dislodgment risk are general features of mussel populations, and other members of the intertidal community. Because the timing of disturbance influences successional processes, such differences may have important consequences for community structure.

Dislodgment in shifting climates

Because large-scale climate changes affect the frequency and severity of storm activity, mussel dislodgment rates may be strongly influenced by shifts in wave climate. Goldenberg *et al.* (2001) report a recent (1995–2000) shift to increased hurricane activity that, because hurricane activity varies on a multidecadal time scale, is likely to persist for 10–40 yr. Carrington (2002) suggests one predicted consequence of such a climate shift is an increased rate of wave-induced disturbance to mussels in Rhode Island, where hurricane season coincides with the months of weakest attachment (September–October). A similar shift in the activity of extratropical storms in this region, which typically occur when mussel attachment strength is greater (October–May), would have less severe consequences.

It is likely, however, that the impact of large-scale climate changes on wave disturbance to intertidal communities will vary regionally. For example, Goldenberg *et al.* (2001) show that during eras of high hurricane activity (1926–1970; 1995–2000), landfalls do not uniformly increase across the North Atlantic, but instead exhibit preferred locations (*e.g.*, the Caribbean and U.S. East Coast). When the frequency of landfalls on the U.S. East Coast is viewed at an even finer scale, activity becomes intensified in specific regions (southern Florida, the Outer Banks of North Carolina, southern New England), but remains unaltered in other regions. Thus it appears that the offshore wave climate of some shorelines may be more closely linked to large-scale climate changes than others. Similar regional patterns in offshore wave climate have been observed by Woolf *et al.* (2002), where the inter-annual variability of winter wave heights is strongly correlated with the North Atlantic Oscillation (NAO) to the north and west of the British Isles, but not to the south or east. While the impacts of such regional variations in wave climate remain unexplored, Ottersen *et al.* (2001) suggest that regional variability is a general feature of the numerous ecological responses to alterations in temperature, wind, and precipitation associated with the NAO.

But what if mussels can respond to shifts in wave climate by altering their attachment strength? While the studies of Price (1982) and Carrington (2002) suggest that the ability of mussels to respond to flow may be energetically constrained in certain seasons, populations may nonetheless be able to respond to chronic (long-term) fluctuations in climate. For example, increased flow may select for genotypes with lower dislodgment risk (those with increased attachment strength and/or reduced shell size). Individuals may be able to achieve the same end by acclimating to gradual changes in wave climate. While the energetic costs associated with reducing dislodgment risk are not known precisely, increased byssal thread production may come at the expense of growth and reproduction. Reduced shell growth may be viewed as a double-

edged sword in that it lowers dislodgment risk (by lowering hydrodynamic loading), but also reduces a mussel's ability to compete for resources (space, food) and escape from size-selective predators.

Variation between species

Finally, there is considerable interspecies variation at all levels of the mechanical design of mussel byssus. While most of the examples presented here are for *M. edulis*, the byssus of *M. californianus* can be considered mechanically superior in a number of regards. In comparison to “*edulis*-like” species (*M. edulis*, *M. trossulus* and *M. galloprovincialis*; McDonald and Koehn, 1988), threads of *M. californianus* are stronger, initially stiffer, more extensible, and more rapid in their recovery of stiffness following deformation (Bell and Gosline, 1996; Carrington and Gosline, 2003). All of these material attributes enhance mussel attachment strength, and likely reflect differences in structure at the molecular level (*e.g.*, Mascolo and Waite, 1986). Furthermore, the morphology of *M. californianus* (relatively thicker threads and reduced shell area) reduces its dislodgment risk (Bell and Gosline, 1997). Thus the mechanical design of *M. californianus* contributes to its ecological success on the most extreme of wave-exposed shores. Further comparative analyses of mussel attachment, conducted at any level of organization, should yield meaningful insights into the relationship between byssus structure and function.

The superior mechanical design of *M. californianus* may reflect (or be reflected in) its life history. For example, increased investment in structural materials can increase longevity (reducing dislodgment risk), but may necessitate slower growth and delayed reproduction. In contrast, *edulis*-like species exhibit a “weedy” life history (relatively rapid growth, early reproduction, and early mortality), perhaps to compensate for their inferior mechanical design (*sensu* Koehl, 1999). While either strategy may be “successful” in a given environment, it is worth noting that life history can influence mechanical design, and *vice versa*.

Conclusion

Byssal attachment is affected by processes that occur at all levels of biological organization, from molecules to ecosystems. From the examples presented here, it is clear that many of these levels of organization are linked, often in complex ways that we are only beginning to understand. For example, water motion not only generates forces that strain byssal threads, but may also provide an environment that enhances the recovery process in deformed threads. Mussels can sense and respond to changes in their flow environment by producing a stronger attachment, but there may be physiological constraints on this mechanical response, which in turn may have important consequences for the ecological response of mussels to shifts in wave climate. Thus an integrative approach to the mechanics of byssal attachment is needed to

fully comprehend this important aspect of the physiological ecology of mussels on rocky intertidal shores.

ACKNOWLEDGMENTS

I thank Frank Gibbons for contributing his data on the tensile properties of mussel byssus, and Mike Boller, Joe Mello, Gretchen Moeser for help in preparing the manuscript. John Gosline, Mark Denny, Herb Waite, and Ken Sebens have provided valuable input on this topic over the years. This material is based upon work supported by National Science Foundation awards OCE-9711893 and OCE-0082605 and by the University of Rhode Island.

REFERENCES

- Bell, E. C. and M. W. Denny. 1994. Quantifying 'wave exposure': A simple device for recording maximum velocity and results of its use at several field sites. *J. Exp. Mar. Biol. Ecol.* 181:9–29.
- Bell, E. C. and J. M. Gosline. 1996. Mechanical design of mussel byssus: Material yield enhances attachment strength. *J. Exp. Biol.* 199:1005–1017.
- Bell, E. C. and J. M. Gosline. 1997. Strategies for life in flow: Tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Mar. Ecol. Prog. Ser.* 159:197–208.
- Brown, C. H. 1952. Some structural proteins of *Mytilus edulis* L. *Quart. J. Micros. Sci.* 93:487–502.
- Carrington, E. 2002. Seasonal variation in the attachment strength of blue mussels: Causes and consequences. *Limnol. Oceanogr.* 47:1723–1733.
- Carrington, E. and J. M. Gosline. 2003. Mechanical design of mussel byssus: Load cycle and strain rate dependence. *Am. Mal. Bull.* (In press)
- Denny, M. W. 1987. Lift as a mechanism of patch initiation in mussel beds. *J. Exp. Mar. Biol. Ecol.* 113:231–245.
- Denny, M. W. 1988. *Biology and the mechanics of the wave-swept Environment*. Princeton University Press.
- Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* 55:69–102.
- Denny, M., B. Gaylord, B. Helmuth, and T. Daniel. 1998. The menace of momentum: Dynamic forces on flexible organisms. *Limnol. Oceanogr.* 43:955–968.
- Denny, M. and D. Wetthey. 2001. Physical processes that generate patterns in marine communities. In M. D. Bertness, S. E. Gaines, and M. E. Hay (eds.), pp. 3–37. *Marine community ecology*. Sinauer Associates, Sunderland, MA.
- Floriolii, R. Y., J. von Langen, and J. H. Waite. 2000. Marine surfaces and the expression of specific byssal adhesive protein variants in *Mytilus*. *Mar. Biotech.* 2:352–363.
- Gaylord, B. 1999. Detailing agents of physical disturbance: Wave-induced velocities and accelerations on a rocky shore. *J. Exp. Mar. Biol. Ecol.* 239:85–124.
- Gaylord, B. 2000. Biological implications of surf-zone complexity. *Limnol. Oceanogr.* 45:174–188.
- Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Núñez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. *Science* 293:474–479.
- Gosline, J., M. Lillie, E. Carrington, P. Guerette, C. Ortlepp, and K. Savage. 2002. Elastic proteins: Biological roles and mechanical properties. *Phil. Trans. Roy. Soc. B* 357:121–132.
- Hawkins, A. J. S. and B. L. Bayne. 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: Budgets, conversion efficiencies and maintenance requirements. *Mar. Ecol. Prog. Ser.* 25:181–188.
- Hunt, H. L. and R. E. Scheibling. 2001. Predicting wave dislodgment of mussels: Variation in attachment strength with body size, habitat, and season. *Mar. Ecol. Prog. Ser.* 213:157–164.
- Koehl, M. A. R. 1999. Ecological biomechanics of benthic organisms: Life history, mechanical design and temporal patterns of mechanical stress. *J. Exp. Biol.* 202:3469–3476.
- Leonard, G. H., M. D. Bertness, and P. O. Yund. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* 80:1–14.
- Mascolo, J. M. and J. H. Waite. 1986. Protein gradients in byssal threads of some marine bivalve molluscs. *J. Exp. Zool.* 240:1–7.
- McDonald, J. H. and R. K. Koehn. 1988. The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America. *Mar. Biol.* 99:111–118.
- McDowell, L. M., L. A. Burzio, J. H. Waite, and J. Schaefer. 1999. REDOR detection of cross-links formed in mussel byssus under high flow stress. *J. Biol. Chem.* 274:20293–20295.
- Niklas, K. J. 1992. *Plant biomechanics*. University of Chicago Press.
- Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1–14.
- Price, H. A. 1982. An analysis of factors determining seasonal variation in the byssal attachment strengths of *Mytilus edulis*. *J. Mar. Biol. Ass. U. K.* 62:147–155.
- Seed, R. and T. H. Suchanek. 1992. Population and community ecology of *Mytilus*. In E. G. Gosling (ed.), *The mussel Mytilus: Ecology, physiology, genetics, and culture*, pp. 87–169. Elsevier Press, New York.
- Suchanek, T. H. 1985. Mussels and their role in structuring rocky shore communities. In P. G. Moore and R. Seed (eds.), *The ecology of rocky coasts*, pp. 70–76. Hodder and Stoughton, Sevenoaks, U.K.
- Sun, C., E. Vaccaro, and J. H. Waite. 2001. Oxidative stress and the mechanical properties of naturally occurring chimeric collagen-containing fibers. *Biophys. J.* 81:3590–3595.
- Vaccaro, E. and J. H. Waite. 2001. Yield and post-yield behavior of mussel byssal thread: A self-healing biomolecular material. *Biomacromolecules* 2:906–911.
- Vogel, S. 1994. *Life in moving fluids*. Princeton University Press.
- Wainwright, P. C. and S. M. Reilly. (eds.) 1994. *Ecological morphology*. University of Chicago Press, Chicago.
- Waite, J. H. 1992. The formation of mussel byssus: Anatomy of a natural manufacturing process. In S. T. Case (ed.), *Results and problems in cell differentiation*, Vol. 19. *Biopolymers*, pp. 27–54. Springer-Verlag, Berlin.
- Waite, J. H., X.-X. Qin, and K. J. Coyne. 1998. The peculiar collagens of mussel byssus. *Matrix Biology* 17:93–106.
- Witman, J. D. 1987. Subtidal coexistence: Storms, grazing, mutualism, and the zonation of kelps and mussels. *Ecol. Monogr.* 57:167–187.
- Witman, J. D. and T. H. Suchanek. 1984. Mussels in flow: Drag and dislodgement by epizoans. *Mar. Ecol. Prog. Ser.* 16:259–268.
- Wolf, D. K., P. D. Cotton, and P. G. Challenor. 2002. Measurements of the offshore wave climate around the British Isles by satellite altimeter. *Phil. Trans. Roy. Soc. London A.* (In press)