

Confronting the physiological bottleneck: A challenge from ecomechanics

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We begin by giving away our punch line: *A lack of physiological insight is the primary impediment to the successful prediction of the ecological effects of climatic change.* To be sure, there are uncertainties in our predictions of future climate, especially at the local scale, and the complexities of ecological interactions stretch our ability to model complex systems. But it is physiology—our understanding of how individual organisms function and interact with their environment—that presents the largest challenge. Without a better mechanistic understanding of how plants and animals work, we can never be assured of an accurate warning of what lies ahead for life on earth.

SICB's Grand Challenges for Organismal Biology (Schwenk et al. 2009) accurately highlight many of the current gaps in our understanding of physiology as it relates to ecological prediction. Addressing these challenges will thus serve to advance our quest to predict the ecological effects of variability in climate.

To justify these conclusions, let us step back and review a bit of academic

history. The field of biomechanics applies the theory and methods of physics and engineering to explain how plants and animals exchange heat, mass, or momentum with their surroundings. At its core, biomechanics assumes a mechanistic, bottom-up approach to science, arguing, in essence, that if one understands the pertinent details of how plants and animals work, one can predict how they will function in any environment. Arguably, biomechanics gelled as a field with the work of Sir James Gray, a zoologist at Cambridge University in England. He applied fluid mechanical theory to the study of aquatic locomotion. (It was Gray who noticed that the power output of dolphins' muscles appeared to be insufficient to propel them at the speed they are observed to swim, a conundrum known as Gray's Paradox that continues to garner interest, e.g. Fish 2006.) From Gray, the biomechanical torch passed first to Torkel Weis-Fogh (also at Cambridge) and then (upon Weis-Fogh's untimely death) to R. McNeill Alexander at Leeds University. Through their research and

that of their students—and especially through Alexander's prolific production of books on the subject—biomechanics expanded from its initial focus on animal locomotion to include elements of materials science, physical chemistry, and structural mechanics. Comparable headway was made in the prediction of organisms' body temperatures through the application of quantitative heat budget models. In the 1970s and 1980s, this broadened field was consolidated and popularized by three classic texts: *Mechanical Design in Organisms* (Wainwright et al. 1976), *Biophysical Ecology* (Gates 1980), and *Life in Moving Fluids* (Vogel 1981). Biomechanics currently stands as a highly successful example of both the mechanistic approach to biology and the potential for interdisciplinary science.

Despite the impressive breadth of its subject matter—from bacteria to blue whales, diatoms to red woods, extant to long extinct species (and despite the title of Gates' tome)—classical biomechanics has traditionally maintained its focus on a single level of

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organization: the individual organism. Recently, however, a few practitioners have begun to extend biomechanics' mechanistic approach across additional levels. The goal of this burgeoning field is to construct mechanistic models that describe not only how individual organisms work, but also how these organisms interact with each other and with their environment, and how changing environmental conditions are likely to affect populations, communities, and the distribution of species. This consolidation of biomechanics and ecology is termed "ecomechanics" (Carrington 2002a, Denny and Gaylord 2010).

The potential of this new field has been demonstrated in several arenas. For example, the pattern of dispersal of spores of the giant kelp *Macrocystis pyrifera* can be predicted as a function of ocean currents and waviness (Gaylord et al. 2002, 2006). These predictions provide ecologists and policy makers with a valuable tool for the appropriate design of marine protected areas on the many coasts where *Macrocystis* is the dominant seaweed. In another example, the spatial distribution and rate of disturbance of three coral species on the Great Barrier Reef can be accurately predicted from historical records of wind speeds. Wind records allow for the prediction of the distribution of wave heights, which in turn can be used to predict maximum velocities and accelerations of water for any spot on the reef (Madin et al. 2006). Knowledge of the hydrodynamic interaction of corals with flow and of the strength of coral skeleton then leads to spatially specific estimates of the rate of disturbance (Madin 2005, Madin and Connolly 2006). In a bold extension of this technique, Madin et al. (2008) predicted the likely shifts in species abundance that will occur when, as a result of large-scale climatic change (IPCC 2007), the waviness of the ocean increases (thereby increasing hydrodynamic forces) and the pH of the ocean decreases (thereby decreasing the strength of the carbonate substratum to which corals attach).

A third example sets the stage for the discussion that follows. Mussels are the

competitive dominant for space on many wave-swept rocky shores, in large part due to their ability to adhere to the substratum with a byssus, a flexible tethering system of proteinaceous threads. The efficacy of the byssus is such that (in the absence of severe hydrodynamic forces or predation that results in chronic disturbance) mussels exclude other primary space occupiers from the shore, drastically reducing the diversity of the intertidal community (Dayton 1971, Seed and Suchanek 1992). But as waves break, they can occasionally apply hydrodynamic forces sufficient to dislodge mussels (Denny 1995). As a result, the community ecology of many wave-swept shores is governed to a great extent by the temporally and spatially variable interaction between the recruitment and growth of mussels and their removal by waves (Paine and Levin 1981). Owing significantly to the work of Emily Carrington and J. Herbert Waite and their colleagues (e.g. Denny 1987; Waite 1992; Bell and Gosline 1996, 1997; Waite et al. 1998; McDowell et al. 1999; Florioli et al. 2001; Lin et al. 2007), we have a wealth of information about the chemistry and material properties of byssal threads, the mechanics of the byssus, and the wave-height-dependent hydrodynamic forces imposed by breaking waves. This information has been used to successfully predict the rate of dislodgment in mussels as a function of wave climate (Carrington et al. 2009), allowing for subsequent prediction of intertidal community dynamics.

This example highlights the potential for ecomechanics to incorporate information at multiple levels of organization—ranging from chemistry, to materials science, to morphology, fluid dynamics and ecology—to make predictions about the structure and dynamics of an important ecological community. But a closer look reveals acute limitations. For example, mussel byssus is a dynamic structure. Individual threads have a limited effective lifetime and are sloughed off as new threads are produced (e.g. Moeser and Carrington 2006). The overall strength of the byssus thus depends, in part, on

the relative rates of thread production and senescence. In addition, the size and chemical composition of individual threads can differ for mussels from different exposures to waves (Carrington 2002b; Moeser et al. 2006; Zardi et al. 2006, 2007; Carrington et al. 2008) and for individual mussels at different times (e.g. Moeser and Carrington 2006). Variation in the combined effects of production, size, and composition of threads are evident in an annual cycle of byssal strength, which tends to be highest in winter and lowest in summer (e.g. Price 1980, Moeser and Carrington 2006).

The problem is that, despite the existence of an obvious annual cycle, we do not know enough about the physiology or time course of the production of threads to be able to predict byssal strength. Some evidence suggests that the cycle of strength is set by the trade-offs between reproduction and byssal renewal: When a mussel is actively growing its gonads, energy may be diverted away from thread production and strength may decrease (Carrington 2002a, b). Reproductive output is affected by body temperature both above water and while submerged, as well as by availability of food, factors that may thus indirectly affect rates of production of byssal threads. Other evidence points to a further role for environmental temperature: When water temperature is high, weaker threads are produced and they senesce more rapidly (Moeser and Carrington 2006). Still other evidence suggests that byssal strength can be a direct function of availability of food and that mussels can adjust byssal strength in response to imposed forces (Zardi et al. 2006, 2007).

Given this variety of potential influences, both direct and indirect, on byssal strength, our ability to predict future rates of mussel dislodgment is seriously limited. If, as expected, the ocean gets warmer and wavier, what will the effect be? We just do not know. Increased temperature might weaken threads while increased wave action might stimulate thread production.

The situation is made even more complex when we consider reproduction

in greater detail. In laboratory experiments, Smith and Strehlow (1983) found that the cue for mussels to spawn was a soluble chemical released by phytoplankton: When phytoplankton concentrations were high, mussels spawned. This interaction might set the timing of the mussel reproductive cycle, and, thereby, the annual cycle of byssal strength. But, in a surprising twist, mussels responded to the chemical cue only when the pH of the water was greater than approximately 8.0. This raises the possibility that, as pH in the ocean decreases due to increased concentration of atmospheric CO₂ (IPCC 2007), mussels' cycle of byssal strength could be drastically altered, potentially changing the temporal relationship between strength of attachment and wave forces, and ultimately leading to altered rates of dislodgment.

Smith's and Strehlow's work provides a daunting and important message. Accurate prediction of the effects of altered climate requires detailed mechanistic understanding of physiology. At present, the pH of the ocean's surface is >8.0, and as a result field experiments under extant conditions can provide no hint of the pH threshold in spawning behavior. It is only through Smith's and Strehlow's search for a mechanistic understanding of spawning physiology that we have a glimpse of this potentially important "switch" in mussel biology.

In short, without a detailed mechanistic understanding of mussel physiology and byssal-thread production, we are stymied in our mission to predict dislodgment of mussels. Ecomechanics can accurately predict everything up to the point at which we need to know byssal strength, and ecological theory can predict the consequences of mussel dislodgment, but because of our limited knowledge of physiology, these two predictions cannot currently be connected. The same physiological bottleneck applies to virtually all examples of ecomechanical application (Helmuth et al. 2005, Helmuth 2009, Denny and Gaylord 2010).

The field of ecomechanics is not without its own challenges. For

example, one of ecomechanics' most pressing tasks is to move from a framework based on explicit mechanism to one based on probability so that we can incorporate individual variation, environmental heterogeneity, and uncertainty in both our understanding of how organisms interact with their environment as well as in predictions of how environments are likely to change (e.g. Denny et al. 2009). However, a key difficulty with this task is, again, that we first require a deeper understanding of physiology at the level of the organism—that is, the level where fitness is determined.

In light of this perceived physiological bottleneck, those of us in the field of ecomechanics applaud Schwenk et al. (2009) for their formulation of Grand Challenges in Organismal Biology. In the process of addressing those five challenges, organismal biologists will go far toward removing ecomechanics' largest stumbling block. As a guide to the physiological community, we list four specific tasks that we view to be the most crucial for ecomechanics and note the Grand Challenges in which they are embedded:

(1) We must understand the role of environmental history on organismal performance in such a way that we can extract generalities (Challenge 1: Understanding the organism's role in organism-environment linkages; Challenge 3: Integrated approach to analysis of living and physical systems). For example, it is well known that the thermal history of an organism affects its tolerance to extremes of temperature (e.g. Buckley et al. 2001). Likewise, as we have noted, exposure to high forces can increase resistance to further insult (Zardi et al. 2006, 2007). However, for most cases we do not yet understand the time course of adaptation and acclimation (Challenge 4: Understanding how genomes produce organisms; Challenge 5: Understanding how organisms walk the tightrope between stability and change), and so cannot predict

physiological performance, even when our measurements of the local environment are precise.

- (2) We require a better understanding of how processes at the cellular and subcellular levels translate into organismal responses (Challenges 1, 3, 4, and 5). Recent advances in molecular techniques have provided a wealth of insight into how changing environments result in responses such as the production of heat shock proteins, and it may well be that a predictive understanding of organism/environment interactions requires information at the fundamental level of genes themselves. However, as we delve deeper into mechanisms at the level of the cell and below, it has become increasingly difficult to scale those results back up to organisms and thus to populations and communities. While the delineation of physiological indicators of stress is a major step forward, these indices need to be better integrated with measurements of fitness.
- (3) Comparison of effects between individuals and between species—especially between predator and prey and between competitors—requires further attention. For example, the concept of "environmental stress models"—the idea that relative levels of stress affecting organisms at different trophic levels drives community ecology—has been tossed about in ecology for quite some time (e.g. Menge and Sutherland 1976). However, only recently have detailed measurements of physiological indicators of stress been brought to bear on this question (e.g. Petes et al. 2008). Predictions of the responses of communities to environmental stress must include species interactions, and so if we are to integrate physiology into community ecology, we must examine both the direct effects of environmental conditions on interacting species (the role of physiology) as well as on the interactions themselves (the role of ecology) (see, for instance, Pincebourde et al. 2008).

(4) Haunting our ecomechanical quest to predict the effects of climatic change are concerns about evolution. Because the organisms of tomorrow might differ from those of today, it seems likely that we could construct a thoroughly detailed mechanistic model of how extant organisms interact with their environment and still fail to make accurate predictions about the future. It is crucial to ecomechanics that organismal biologists be able to predict the rate at which organisms can adapt to environmental change and the extent to which this occurs (Challenges 4 and 5).

In sum, the combined fields of ecomechanics and physiology are likely to provide a powerful tool for confronting the complex effects posed by global climatic change. To make the partnership work, however, we must develop methods that strive toward a common focus—that of the organism. Only then can we break through the current bottleneck and examine the range of scales necessary to predict what the future is likely to hold.

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