

# ECOLOGICAL BIOMECHANICS OF BENTHIC ORGANISMS: LIFE HISTORY, MECHANICAL DESIGN AND TEMPORAL PATTERNS OF MECHANICAL STRESS

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## Summary

**We can gain biomechanical insights if we couple knowledge of the environments, ecological roles and life history strategies of organisms with our laboratory analyses of their mechanical function or fluid dynamics, as illustrated by studies of the mechanical design of bottom-dwelling marine organisms. Obviously, measurements of the spatial and temporal distribution of loads on an organism in nature reveal the magnitudes and rates at which biomechanical tests should be performed in the laboratory. Furthermore, knowledge of the population biology and ecological interactions of the organisms being studied is crucial to determine when during the life of an individual particular aspects of mechanical performance**

**should be measured; not only can the size, shape and material properties of an individual change during ontogeny, but so can its habitat, activities and ecological role. Such ecological information is also necessary to determine whether the aspects of mechanical performance being studied are biologically important, i.e. whether they affect the survivorship or fitness of the organisms. My point in raising these examples is to illustrate how ecological studies can enhance or change our understanding of biomechanical function.**

Key words: kelp, ascidian, sea anemone, wave, spawning, canopy, biomechanics, size, life history, benthos.

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## Introduction

Processes operating at the level of individual organisms can determine the properties of populations, communities and ecosystems (e.g. Schoener, 1986; May et al., 1989); hence, biomechanics can provide useful tools to address ecological questions (for reviews, see Koehl, 1989, 1996, 1998; Jumars, 1993; Wainwright and Reilly, 1994). Biomechanical studies have shown that general physical rules that apply across taxa can permit us to understand and predict how organisms interact with their physical environments (for reviews, see Alexander, 1983; Koehl, 1984; Denny, 1988; Niklas, 1992). Similarly, since the performance of an organism is the crucial link between its phenotype and its ecological success, organism-level mechanistic analyses of how function depends on biological form have revealed morphological constraints not only on habitat use but also on ecological interactions, such as competition or predation, and on reproductive strategies.

My purpose in this paper is not to chronicle further the role of biomechanics as the 'handmaiden' (*sensu* Wake, 1982) of ecology, but rather to focus on the converse: how ecological information can aid biomechanical research. For example, measurements of the spatial and temporal distribution of environmental factors (e.g. water flow, biting predators, shoving neighbors) that impose mechanical loads on an organism reveal the magnitudes and rates at which biomechanical analyses should be performed in the laboratory

(e.g. in flumes or materials testing devices). Furthermore, knowledge of the life history and ecological interactions of the organisms being studied is crucial not only to assess when during the life of an individual various aspects of mechanical performance should be measured (size, shape and material properties can change during ontogeny, as can the habitat, activities and ecological role of an individual) but also to determine whether the aspects of mechanical performance being studied affect the survivorship or fitness of the organisms. In this paper, I will describe a few examples involving benthic marine organisms that illustrate how biomechanical insights can be provided by ecological information. I will first discuss examples of how the mechanical responses of the tissues of organisms depend on the temporal patterns of loading they experience in their natural microhabitats. I will then examine a few cases of how our understanding of the biomechanical scaling of organisms as they grow can be changed when considered in the context of their distribution in the field and their population ecology. Finally, I will provide some examples of how an appreciation of the life history strategies of organisms with 'bad' engineering designs enable us to understand how they can thrive in mechanically stressful environments. My point in raising these examples is to illustrate how ecological studies can enhance or change our understanding of biomechanical issues.

### Duration and rate of mechanical loading in nature

An important area of biomechanical research is the study of the material properties of biological tissues. Many soft connective tissues show viscoelastic mechanical behavior. A classic example is the mesoglea of sea anemone body wall, which Alexander (1962) modeled over three decades ago by a combination of springs (simulating the elastic behavior of solids whose resistance to deformation is a function of stress, the force per cross-sectional area they bear) and dashpots (simulating the viscous behavior of fluids whose resistance to deformation depends on the rate at which they are deformed). His study set the stage for using mesoglea as a system to work out the macromolecular mechanisms responsible for such viscoelastic behavior in collagenous connective tissues (Gosline, 1971a,b). However, the biological significance of the viscoelastic properties of mesoglea can be understood only by considering the rates and durations of stresses in this tissue in sea anemones in nature.

Sea anemones, which live attached to the substratum in the ocean, are hydrostatically supported animals composed of a tensile bag of connective tissue, the mesoglea, surrounding a water-filled gastrovascular cavity. To assess how the performance of sea anemones might be affected by the time-dependent properties of their mesoglea, I subjected mesoglea from different species to a series of mechanical tests designed to simulate the rates and durations of various stresses in these animals in nature (Koehl, 1977b). To design these tests, however, I first had to quantify the time course of the hydrodynamic forces on the animals in their respective microhabitats as well as the behaviors and shape changes they undergo under field conditions (Koehl, 1977a,c). *Anthopleura xanthogrammica* live on rocky shores in surge channels where they are subjected to the back-and-forth water flow of waves. When subjected to stress regimes simulating those in an anemone in waves, the mesoglea from *A. xanthogrammica* recoils to resting length between successive 'waves'. Thus, the time-dependent properties of this mesoglea permit *A. xanthogrammica* to maintain their upright body posture during hours of exposure to wave action; in this posture, they can capture mussels and sea urchins washed down onto them from the rocks above. In contrast, the mesoglea from *Metridium senile*, a species that lives in deeper water at sites exposed to tidal currents rather than waves, recoils more slowly. When subjected to stress regimes simulating those it would encounter if it lived in the wave-swept habitat of *A. xanthogrammica*, the mesoglea of *M. senile* does not fully recover to its unstressed shape before the next 'wave' hits, but becomes successively more stretched out with each cycle of loading.

Although not suitable for shape-maintenance on wave-beaten shores, the viscoelastic properties of the mesoglea of *M. senile* do contribute to successful foraging by this species in the gentle tidal currents it encounters in its own habitat. When exposed to steady stress over the time scale of several hours (simulating stress due to hydrodynamic drag on an animal in a tidal current), the mesoglea becomes more compliant than when subjected to loads lasting seconds to minutes, as during

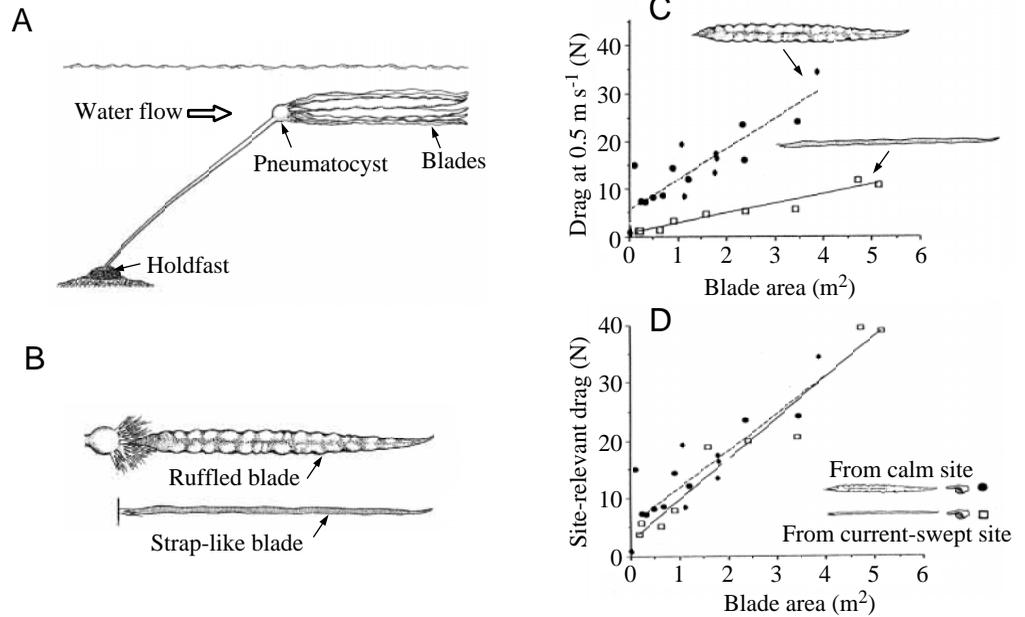
muscle contraction. On the time scale of a few hours, *M. senile* are bent over by the flow as their upstream sides stretch. As they bend, their suspension-feeding crowns of tentacles are passively oriented at right angles to the current, thereby increasing the volume of water they can filter per time for their zooplankton prey. Furthermore, when subjected to small stresses lasting 12–24 h that mimic those due to the low internal pressures produced by the ciliary pump that *M. senile* use to inflate themselves, the mesoglea undergoes extensions of 200–300%. Thus, a single material can serve a variety of skeletal functions requiring different material properties if those functions occur on different time scales: to the muscles of *M. senile*, the mesoglea is relatively stiff (thereby permitting shape changes of the whole hydrostatic skeleton, rather than local bulges, to occur when muscles contract); to the tidal currents, it is more deformable; to the ciliary pump, it is extremely compliant. Comparison of the time-dependent behavior of mesoglea from *M. senile* and *A. xanthogrammica* illustrates how the functional consequences of the material properties of organisms depend on the temporal patterns of loading in different habitats.

Other examples of the importance of making field measurements of the temporal patterns of mechanical loads on biological materials are provided by sessile organisms attached to the substratum by stretchy, resilient tethers such as the stipes of kelp or the byssal threads of mussels. For example, extensible kelp stipes can act as shock absorbers whose stretching absorbs mechanical work, thereby permitting the kelp to withstand the transient high loads they encounter in turbulent or wave-swept habitats; loads of longer duration, however, can stretch these tethers beyond their breaking strains (Koehl and Wainwright, 1977). A wave-swept organism attached to the substratum by a tether can be jerked to a halt if it reaches the end of its rope before the water in a wave begins to flow back in the opposite direction. When this occurs, a brief inertial force pulls on the tether. Mathematical models suggest that the tuning of the time-dependent material properties of stretchy tethers relative to the frequencies at which these structures must resist high inertial loads in wave-swept environments can have a big effect on their likelihood of experiencing large forces (Denny et al., 1998).

### Growth, scaling and changes in physical environment

Another active area of biomechanical research is the study of the consequences of body size. Alexander (1971) outlined many of the physical consequences for organisms of being different sizes. Numerous studies of body size have explored how morphological proportions scale such that function is maintained at different sizes or have sought mechanistic explanations for patterns in how features such as shape or metabolic rate vary with body size (e.g. McMahon and Bonner, 1983; Schmidt-Nielsen, 1984). Changes in body size can occur during the lifetime of an individual organism as it grows or over many generations during the evolution of a lineage; the functional consequences of changing size are reviewed by

Fig. 1. The 'giant bull kelp' *Nereocystis luetkeana*. (A) Diagram of a kelp in a tidal current. (B) Diagram of a ruffled blade and a strap-like blade, each 2 m long. (C) Drag force measured on kelp with ruffled blades (filled circles,  $r^2=0.84$ ,  $P=0.0001$ ) or strap-like blades (open squares,  $r^2=0.94$ ,  $P=0.0001$ ), towed at  $0.5 \text{ m s}^{-1}$ , plotted as a function of the total area of blades on a plant. (D) Drag force on kelp towed at the peak velocity encountered at the site from which each was collected during the week it was collected (calm,  $r^2=0.84$ ,  $P=0.0001$ ; current-swept,  $r^2=0.94$ ,  $P=0.0001$ ) (redrawn from figures in Johnson and Koehl, 1994). Lines represent linear regressions.



Koehl (1999). Benthic marine organisms provide examples of the importance of incorporating information about the field distribution and population ecology of organisms in analyses of the functional consequences of their scaling as they grow.

#### *Ontogenetic scaling of tensile kelp in tidal currents: environmental stress factor*

Much of the work on the biomechanics of size and scaling has focused on terrestrial organisms such as trees, vertebrates and insects, whose skeletal elements are loaded as bending beams or columns by the weight of the organism (e.g. McMahon and Bonner, 1983; Niklas, 1994). In contrast, giant kelp such as *Nereocystis luetkeana* provide useful systems for exploring the scaling of tensile structures. The blades of *N. luetkeana* are supported by a gas-filled float (pneumatocyst) tethered to the substratum by a stipe that is pulled by drag force on the blades when these kelp are exposed to tidal currents (Fig. 1A) (Koehl and Wainwright, 1977; Johnson and Koehl, 1994). For tensile stress in the stipe ('stress similarity') and deformation of the stipe relative to its length ('elastic similarity') to be maintained as such kelp grow, stipe diameter ( $d$ ) should scale as blade area ( $A_B$ ) raised to the 0.5 power (Peterson et al., 1982) assuming that stipe material properties do not change during ontogeny and that drag is proportional to  $A_B$ . However, measurements of *N. luetkeana* showed that they did not follow the predicted scaling law (Johnson and Koehl, 1994): in a population that had flat, narrow, strap-like blades,  $d \propto A_B^{0.3}$ ; for other populations that had wide, ruffled blades,  $d \propto A_B^{0.1-0.2}$  (Fig. 1B). The rate of increase in drag as a function of  $A_B$  at a given velocity was greater for the ruffled kelp than for the strap-like kelp (Fig. 1C), suggesting that the hydrodynamic 'price' for growth was higher for kelp bearing ruffled blades than for those bearing strap-like blades.

Field studies of the hydrodynamics and morphology, coupled with ecological studies of the distribution, growth and

mortality patterns of *N. luetkeana* (Koehl and Wainwright, 1977; Koehl and Alberte, 1988; Johnson and Koehl, 1994), provided insights about the ontogenetic scaling of these kelp. Field surveys and transplant studies revealed that the blades of kelp in habitats exposed to rapid tidal currents took on the flat, strap-like morphology, while those at sites protected from rapid, steady water flow took on the ruffled morphology. Measurement of peak ambient water velocities encountered by *N. luetkeana* blades in the field in their respective habitats permitted site-relevant drag to be measured; the hydrodynamic consequences of growth in  $A_B$  in nature was found to be similar for both blade morphologies (Fig. 1D). We also found that the material properties of the stipe changed during the ontogeny of the kelp and varied between field sites; this result illustrates that the assumption of constant material properties that underlies so many scaling equations is not necessarily valid. By monitoring how stipe breaking stress, site-relevant drag and kelp dimensions varied seasonally during the ontogeny of *N. luetkeana* in populations at different field sites, we found that the 'environmental stress factor' was the same at all the sites and was maintained as the kelp grew during the summer months when they were subjected to tidal currents, but did not experience storms (Fig. 2). The environmental stress factor is the ratio of the strength (the stress required to break) of a tissue of an organism at a particular stage in its life to the maximum stress it experiences in its natural habitat at that stage in its life (*sensu* Johnson and Koehl, 1994). However, in late autumn after the period of peak spore production for these annual kelp, we found that the environmental stress factor decreased from 12 to 3; this decrease in environmental stress factor was due both to an increase in peak water velocities during seasonal storms and to an accumulation of damage to the stipes as kelp growth rates declined. Indeed, many kelp broke during the autumn when one stipe bore the drag on several kelp tangled together or when grazing sea urchins damaged stipes.

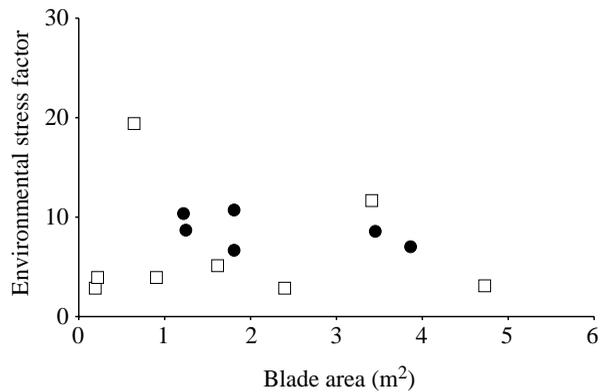


Fig. 2. Environmental stress factor (defined in the text) plotted as a function of total blade area on a kelp for *Nereocystis luetkeana* with ruffled blades from a site exposed to slow ambient water currents (filled circles) and for *N. luetkeana* with strap-like blades from a site exposed to fast ambient water currents (open squares) (redrawn from Johnson and Koehl, 1994). Environmental stress factor is independent of blade area (Kendall's  $\tau$ ,  $P > 0.19$ ).

Alexander (1981) changed our thinking about 'safety factor' (the ratio of the strength of the material in a structure to the maximum stress it experiences during its lifetime) for biological structures by reformulating the concept in terms of the distributions of strengths and maximum stresses in populations of organisms. This approach made analysis of the evolution of safety factors possible. Our ecological studies of *N. luetkeana* revealed that not only did maximum stress and tissue strength vary during the life of an organism, but so did the fitness consequences of failure. This ecological information led us to build on Alexander's safety factor idea to propose the 'environmental stress factor'. Since ambient forces on sessile organisms often vary with season, and since the activities (e.g. foraging patterns, predator avoidance strategies, migration, social interactions and fighting) of motile animals often change with age, the environmental stress factor relates the ability of organisms at their particular stages in ontogeny to resist breakage relative to the maximum loads that they experience in nature at those stages. Environmental stress factor is simply an age- and season-dependent safety factor.

#### Temporal pattern of loading and body size: kelp in waves

Many macroalgae live at sites exposed to wave action rather than to unidirectional currents. Water in waves accelerates back and forth, as does water from broken waves rushing shoreward and then back seaward (e.g. Koehl, 1977a, 1982, 1984). The drag and lift forces on organisms exposed to such oscillatory flow are proportional to the square of the instantaneous water velocity relative to the organism and to the projected area of the organism (proportional to length<sup>2</sup>), while the acceleration reaction force depends on the instantaneous water acceleration relative to the organism and on body volume (proportional to length<sup>3</sup>) (e.g. Koehl, 1977a; Denny et al., 1985). A flexible organism such as a seaweed is bent over and reconfigured by moving water such that its projected area (and hence drag) is

reduced (e.g. Koehl, 1977a). A flexible organism in waves also experiences lower than ambient water velocities and accelerations relative to the portions of its body that are moving with the flow; hence, the force on its holdfast can remain low until the organism is fully extended in the direction of flow and the water moves relative to it (Koehl, 1984, 1996). Furthermore, when the organism reaches the end of its tether, it is jerked to a halt and its attachment organ must bear an inertial force (proportional to body mass, length<sup>3</sup>) (Denny et al., 1998).

The consequences of body length for the forces a flexible organism experiences in waves depend on the distance ( $x$ ) that the water in a wave flows in one direction before it stops and accelerates in the opposite direction. The length of a flexible organism relative to  $x$  determines when in the wave cycle the organism is jerked to a halt and begins to experience flow relative to its body. As flexible organisms that are short relative to  $x$  grow, the total force they experience in waves increases (e.g. Gaylord et al., 1994). However, once organisms grow long enough relative to  $x$  that they only reach the end of their rope after the water in a wave has begun to decelerate, further growth does not lead to an increase in force on the holdfast, as our experiments with model organisms in an oscillating-flow tank have shown (Koehl et al., 1991; Koehl, 1996).

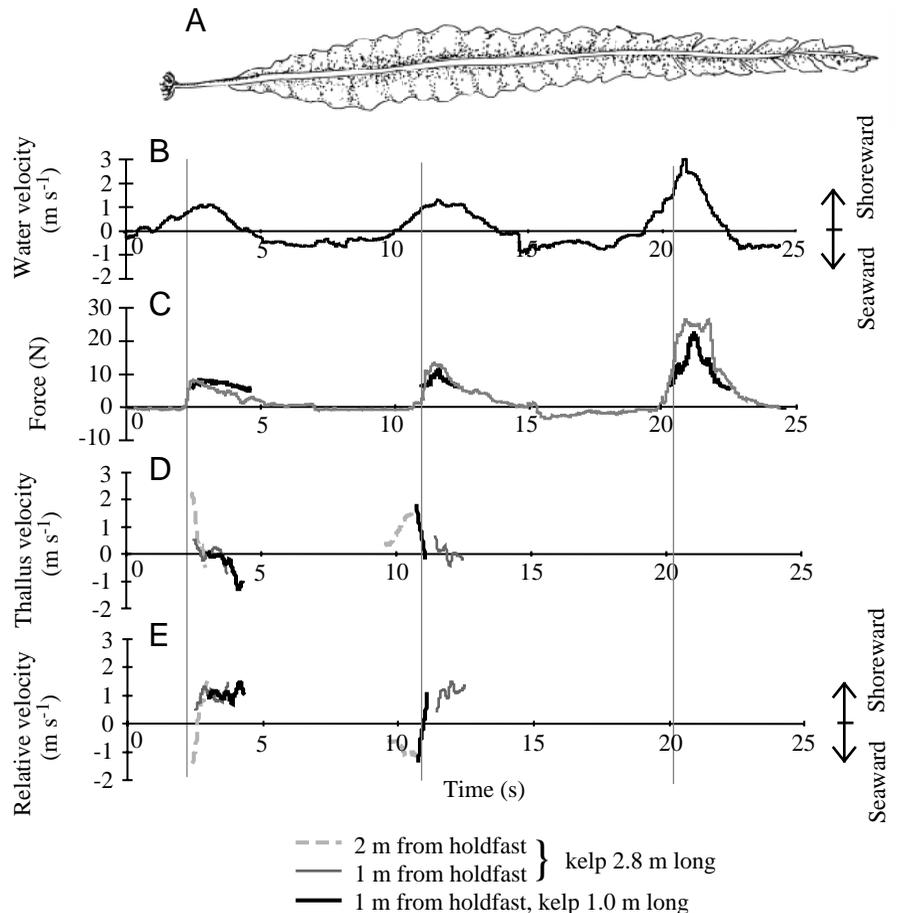
The kelp *Alaria marginata* (Fig. 3A), which live in the low intertidal zone of wave-exposed shores, are an example of an organism that is long relative to  $x$  in its habitat. We attached *A. marginata* of different lengths to force transducers affixed to the shore in their natural habitats and simultaneously measured water velocity, force and motions of marked positions along the kelp (M. A. R. Koehl and T. Cooper, unpublished data). An example of our results is shown in Fig. 3B–D. Peak forces on kelp 1 m and 2.8 m in length attached side-by-side to the shore (Fig. 3C) occurred when the water velocity peaked (Fig. 3B). The shorter kelp was fully strung out when peak water velocity was reached, while the longer kelp was not (Fig. 3D,E). Nine replicates of long and short kelp mounted on force transducers side-by-side on the shore showed that an increase in length of nearly threefold did not lead to a significant increase in the force on *A. marginata* under wave conditions in which they were long relative to  $x$  (M. A. R. Koehl, unpublished data).

These examples illustrate that an increase in body size can increase, decrease or have no effect on the hydrodynamic forces that must be withstood by the holdfast of a flexible organism, depending on the length of the organism relative to the value of  $x$  of the waves. Since wave conditions vary between sites, scaling rules can be habitat-dependent for such organisms. Furthermore, since wave conditions vary from day to day and change with season, it is critical to know the temporal patterns in the field both of the growth of the organisms and of the wave characteristics to work out the mechanical scaling of flexible, wave-swept organisms.

#### Consequences of body size for gamete dispersal during spawning

Not only do sessile benthic organisms have to withstand forces

Fig. 3. The kelp *Alaria marginata*. (A) Diagram of a kelp 3 m in length. (B) Water velocity relative to the shore recorded using an electromagnetic water current meter (Marsh-McBirney, model 511) at the wave-swept site in which two kelp (one 1 m and the other 2.8 m in thallus length) were affixed to force transducers (described in Koehl, 1977a) bolted to the rock substratum. (C) Force at the holdfast on the 1 m kelp (black line) and the 2.8 m kelp (grey line) measured simultaneously with the flow shown in B. (D) Velocity of plastic markers attached to the kelp (thallus velocity relative to the shore) digitized from video recordings made simultaneously with the velocity and force recordings in B and C. Breaks in the recording occurred when foam in the water obscured the view of the markers. (E) Water velocity past the thallus relative to the marked positions on the kelp, calculated from the data shown in B and D. The key below the graphs indicates the positions of the markers plotted in D and E.



imposed on them by ambient water flow, but they also depend on that water motion for the transport of materials (e.g. food, oxygen, gametes, larvae) to and from them. We used physical models of sessile organisms of different sizes releasing dye to assess the dispersal and mixing of spawned gametes or released larvae (techniques described in Koehl et al., 1993; Koehl and Powell, 1994). We found that the consequences of the height of an organism for the dispersal of material it shed into the ambient water flow depended on the biotic and abiotic habitat of the organism. On wave-swept rocky shores, height had no effect on dispersal for solitary organisms, but it did for those surrounded by canopies of flexible macroalgae. In the latter case, the whiplashing back and forth near the substratum of the algae in the waves stirred the water, thereby spreading material released by short organisms more quickly than material released by organisms that stood taller than the flailing algae (Koehl et al., 1996). Conversely, height had the opposite effect on the dispersal of released material for organisms in a rigid coral canopy from that for those in a flexible macroalgal canopy: mixing was greater for material released above the coral canopy than within it (Koehl et al., 1998). In contrast, communities of short, stiff calcified turf-forming algae did not affect the dispersal of released material in a coral reef lagoon (Koehl et al., 1997).

#### *Consequences of body size for suspension feeding*

Bryozoan colonies provide another example of how the

consequences of size depend on habitat (Okamura, 1984, 1985). An increase in colony size can lead to a decrease in the rate of capture of food particles per zooid in habitats characterized by slow ambient currents, as upstream zooids deplete the water of food. However, in habitats exposed to rapidly flowing water, colony growth has the opposite effect on feeding rates per zooid: larger colonies are more effective than smaller ones at slowing the water flowing through them enough (in arborescent colonies) or in diverting flow towards zooids sufficiently (in encrusting colonies) that the zooids are able to catch and hold onto food particles.

As the examples cited above illustrate, the performance consequences of body size can depend on habitat, season and life history stage. Therefore, analyses of size and scaling should be performed in the context of the environment in which the organisms live. Furthermore, the habitat-dependence of the effects of size suggests that, when organisms disperse to new habitats or when the environment changes, selection on body size can change.

#### **'Bad' engineering designs and life history**

Biomechanical techniques permit us to assess whether the morphologies of organisms optimize the performance of particular mechanical functions, as Alexander (1982) summarized so clearly. Biomechanics can also reveal whether

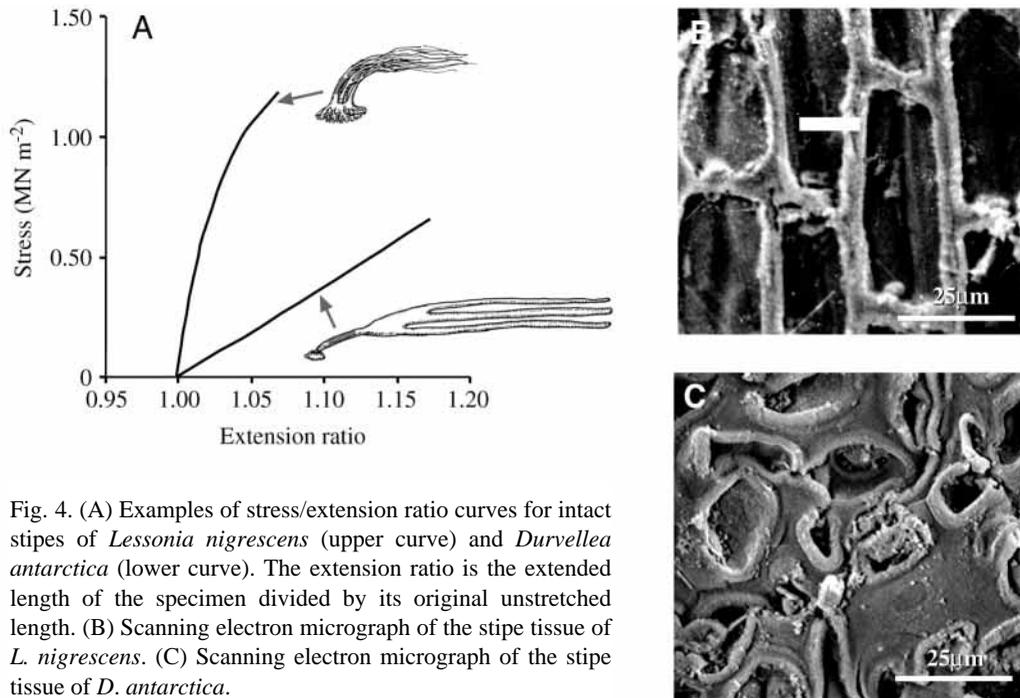


Fig. 4. (A) Examples of stress/extension ratio curves for intact stipes of *Lessonia nigrescens* (upper curve) and *Durvella antarctica* (lower curve). The extension ratio is the extended length of the specimen divided by its original unstretched length. (B) Scanning electron micrograph of the stipe tissue of *L. nigrescens*. (C) Scanning electron micrograph of the stipe tissue of *D. antarctica*.

defined aspects of morphology are important to specific functions (Koehl, 1996). In some cases, biomechanical analyses reveal that the morphologies of organisms lead to poor mechanical performance, but ecological studies can help us understand how such organisms survive and reproduce. Attached marine organisms provide a number of examples of seemingly 'bad' engineering designs that nonetheless thrive in mechanically stressful environments.

#### *Life history can compensate for 'bad' engineering*

*Lessonia nigrescens* and *Durvella antarctica* are large seaweeds that live intertidally on the rocky coast of Chile, where they are exposed to crashing waves (Santelices et al., 1980; Koehl, 1982). The mechanical design of *L. nigrescens* seems to be well-suited to minimize the chances of being broken by waves, whereas that of *D. antarctica* does not. The stipe tissue of *L. nigrescens*, which is composed of closely packed cells with thick cell walls aligned along the major stress axes of the tissue (Fig. 4B) is stiffer and stronger (has a higher breaking stress) (Fig. 4A) than the stipe tissue of *D. antarctica*, which is composed of thin-walled cells that are not aligned and that have large areas of compliant intercellular matrix between them (Fig. 4C) (Koehl, 1986). Furthermore, *L. nigrescens* bears its small, strap-like blades on many wide stipes attached to the substratum by a large, robust holdfast, whereas the thick, wide thallus of a *D. antarctica* is borne by only one stipe attached by a small holdfast. These morphological differences suggest that hydrodynamic forces should induce higher stresses in stipes and holdfasts of *D. antarctica* than in those of *L. nigrescens* (Santelices et al., 1980).

Analysis of the biomechanical performance of these two species of seaweed in the field (Koehl, 1982, 1984, 1986), coupled with a study of their population ecology (Santelices et

al., 1980), revealed how both thallus designs can persist on wave-swept shores. Field measurements of the hydrodynamic forces transmitted to the holdfasts of both species under non-storm conditions showed that *D. antarctica*, whose very long, stretchy thalli were not fully extended in the direction of the flow before the water in the waves changed direction (explained above), experienced forces of similar magnitude to those on *L. nigrescens*. Furthermore, field observations of how the two species of seaweed deformed in waves revealed that the stipes of the upright *L. nigrescens* were bent, whereas those of *D. antarctica*, which have a flexible joint at the holdfast, were pulled. Maximum stresses in a stipe pulled by a load at its end are much lower than those in a stipe bent by the same load. Nonetheless, in the large waves of winter storms, *L. nigrescens* were predicted to survive while *D. antarctica* were predicted to be fully extended in the direction of flow and to experience stresses large enough to break their stipes. Indeed, ecological surveys showed that greater proportions of *D. antarctica* than of *L. nigrescens* were ripped off the shore during winter storms (the *L. nigrescens* that broke usually failed at regions in their stipes and holdfasts that had been damaged by grazers and boring organisms living within them). Nonetheless, *D. antarctica* were successful on wave-swept shores because they recruited year-round when bare space became available on the shore, grew rapidly and produced their propagules before seasonally predictable storms ripped them off the substratum. In contrast, the slower growing *L. nigrescens* recruited only seasonally, took longer after settlement to begin spore production, lived for several years and could regrow after being pruned by wave action and grazing.

These two seaweeds illustrate a pattern seen in many other species (e.g. other macroalgae, Koehl, 1986; barnacles, Murdock and Currey, 1978) that populations of organisms can

persist in mechanically stressful habitats (where they are exposed to, for example, rapid water flow, crushing predators) either by having body designs and material properties that reduce their probability of breakage (i.e. by having a high safety factors *sensu* Alexander, 1981) or by having 'weedy' life history strategies (characterized by opportunistic recruitment, rapid growth and early reproduction) that increase their probability of reproducing before mechanical failure occurs.

#### *Mechanical failure can enhance ecological performance*

The Caribbean stony coral *Acropora cervicornis* provides an example of how 'bad' engineering designs can sometimes enhance the ecological performance of organisms. Tunnicliffe's (1980) biomechanical analysis predicted that these corals, with their long, slim branches (a stress-enhancing shape) supported by brittle skeletal material, should break in rapid water flow, and yet she found that they thrived on wave-swept forereefs. Her population study of *A. cervicornis* showed that they did break often, but that the broken-off pieces survived and grew. Such programmed breakage and growth was the main mechanism of asexual reproduction and dispersal of *A. cervicornis* colonies as well as of a number of other species of breakable coral (Highsmith, 1982). Hence, breakability is not necessarily a 'bad' feature preventing organisms from succeeding in wave-swept environments if those broken organisms can regrow. Furthermore, when bits of such an organism or colony break off, the hydrodynamic forces on the part of the structure that remains can be reduced; hence, partial breakage can prevent total destruction. An example of the latter is provided by the wave-swept kelp *Egregia laevigata*, which break at regions damaged by limpet grazing. Kelp 'pruned' in this way are less likely to wash away during storms than are those not subjected to limpet grazing (Black, 1976).

Conversely, organisms with 'good' mechanical designs can fail to survive mechanically stressful events in certain microhabitats. For example, when Hurricane Allen hit Jamaican coral reefs, the skeletons of large mound-like corals (which have stress-minimizing shapes; Koehl, 1984) did not break, nor did the tough, flexible skeletons of sea fans (Woodley et al., 1981). However, many of the corals and gorgonians living adjacent to sand patches did not survive the hurricane because their living tissue was abraded away by the sand suspended in the water during the storm.

A different group of benthic colonial animals, compound ascidians, provides another example of mechanical failure enhancing ecological performance. Compound ascidians compete effectively for space in benthic and epiphytic communities by overgrowing other organisms (e.g. Nandakumar et al., 1993). If the organisms overgrown by such an ascidian colony senesce and break, then loose flaps of the ascidian colony can be pushed by ambient water flow. The glue by which the fleshy colonies of *Botrylloides* sp. attach to the substratum is very weak, so that colonies can be peeled off the substratum by ambient currents. However, failure of this weak glue protects the soft tissues of the colonies from damage when they are dislodged from the substratum (Edlund and Koehl,

1998). Nonetheless, sessile organisms using such a weak-glue mechanism of preventing tissue tearing can persist only if they are able to reattach to the substratum. *Botrylloides* sp. are able to reattach by rapid growth of new sticky surfaces (Edlund and Koehl, 1998). Thus, even though the larvae of *Botrylloides* sp. only disperse a few meters from their parents, the weak glue of this species permits them to be effective colonists of new sites *via* adult rafting and reattachment (Worcester, 1994).

These examples illustrate an important ecological lesson for biomechanists: in some ecological contexts, 'bad' mechanical designs can fare quite well. We need to know about the life history strategies and ecological interactions of the organisms, as well as the predictability and timing of disturbance events, before we can assess how well-suited various material properties and skeletal designs are to particular environments.

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#### References

- Alexander, R. McN. (1962). Visco-elastic properties of the body wall of sea anemones. *J. Exp. Biol.* **39**, 373–386.
- Alexander, R. McN. (1971). *Size and Shape*. London: Edward Arnold.
- Alexander, R. McN. (1981). Factors of safety in the structure of animals. *Sci. Prog.* **67**, 109–130.
- Alexander, R. McN. (1982). *Optima for Animals*. London: Edward Arnold.
- Alexander, R. McN. (1983). *Animal Mechanics*, 2nd edition. Oxford: Blackwell Scientific Publication.
- Black, R. (1976). The effects of grazing by the limpet, *Acmaea insessa*, on the kelp *Egregia laevigata*, in the intertidal zone. *Ecology* **57**, 65–77.
- Denny, M. W. (1998). *Biology and the Mechanics of the Wave-Swept Environment*. Princeton: Princeton University Press.
- Denny, M. W., Daniel, T. and Koehl, M. A. R. (1985). Mechanical limits to the size of wave-swept organisms. *Ecol. Monogr.* **55**, 69–102.
- Denny, M., Gaylord, B., Helmuth, B. and Daniel, T. (1998). The menace of momentum: Dynamic forces on flexible organisms. *Limnol. Oceanogr.* **43**, 955–968.
- Edlund, A. F. and Koehl, M. A. R. (1998). Adhesion and reattachment of compound ascidians to various substrata: weak glue can prevent tissue damage. *J. Exp. Biol.* **201**, 2397–2402.
- Gaylord, B., Blanchette, C. A. and Denny, M. W. (1994). Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* **64**, 287–313.

- Gosline, J. M.** (1971a). Connective tissue mechanics of the sea anemone *Metridium senile*. I. Structural and compositional aspects. *J. Exp. Biol.* **55**, 763–744.
- Gosline, J. M.** (1971b). Connective tissue mechanics of the sea anemone *Metridium senile*. II. Visco-elastic properties and macromolecular model. *J. Exp. Biol.* **55**, 775–795.
- Highsmith, R. C.** (1982). Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* **7**, 207–226.
- Johnson, A. J. and Koehl, M. A. R.** (1994). Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: thallus allometry and material properties of a giant kelp. *J. Exp. Biol.* **195**, 381–410.
- Jumars, P. A.** (1993). *Concepts in Biological Oceanography: An Interdisciplinary Primer*. Oxford: Oxford University Press.
- Koehl, M. A. R.** (1977a). Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.* **69**, 87–105.
- Koehl, M. A. R.** (1977b). Mechanical diversity of the connective tissue of the body wall of sea anemones. *J. Exp. Biol.* **69**, 107–125.
- Koehl, M. A. R.** (1977c). Mechanical organization of cantilever-like sessile organisms: sea anemones. *J. Exp. Biol.* **69**, 127–142.
- Koehl, M. A. R.** (1982). The interaction of moving water and sessile organisms. *Scient. Am.* **247**, 124–132.
- Koehl, M. A. R.** (1984). How do benthic organisms withstand moving water? *Am. Zool.* **24**, 57–70.
- Koehl, M. A. R.** (1986). Seaweeds in moving water: Form and mechanical function. In *On the Economy of Plant Form and Function* (ed. T. J. Givnish), pp. 603–634. Cambridge: Cambridge University Press.
- Koehl, M. A. R.** (1989). From individuals to populations. In *Perspectives in Ecological Theory* (ed. R. M. May, J. Roughgarden and S. A. Levin), pp. 39–53. Princeton, NJ: Princeton University Press.
- Koehl, M. A. R.** (1996). When does morphology matter? *Annu. Rev. Ecol. Syst.* **27**, 501–542.
- Koehl, M. A. R.** (1998). Physiological, ecological and evolutionary consequences of the hydrodynamics of individual organisms. *OEUVRE*, [http://www.joss.ucar.edu/joss\\_psg/project/oce\\_workshop/oeuvre/](http://www.joss.ucar.edu/joss_psg/project/oce_workshop/oeuvre/)
- Koehl, M. A. R.** (1999). Consequences of size changes. In *Scaling in Biology* (ed. J. H. Brown and G. B. West). Oxford: Oxford University Press (in press).
- Koehl, M. A. R. and Alberte, R. S.** (1988). Flow, flapping and photosynthesis of macroalgae: Functional consequences of undulate blade morphology. *Mar. Biol.* **99**, 435–444.
- Koehl, M. A. R., Dobbins, E., Best, B. A., Merz, R. and Moore, S.** (1998). Small-scale mixing and transport in and above a coral reef during mass spawning. *Eos Trans. Am. Geophys. Union* (Suppl.) **79**, OS165.
- Koehl, M. A. R., Hunter, T. and Jed, J.** (1991). How do body flexibility and length affect hydrodynamic forces on sessile organisms? *Am. Zool.* **31**, 60A.
- Koehl, M. A. R. and Powell, T. M.** (1994). Turbulent transport of larvae near wave-swept shores: Does water motion overwhelm larval sinking? In *Reproduction and Development of Marine Invertebrates* (ed. H. Wilson, G. Shinn and S. Stricker), pp. 261–274. Baltimore, MD: Johns Hopkins University Press.
- Koehl, M. A. R., Powell, T. M. and Dairiki, G.** (1993). Measuring the fate of patches in the water: Larval dispersal. In *Patch Dynamics in Terrestrial, Marine and Freshwater Ecosystems* (ed. J. Steele, T. M. Powell and S. A. Levin), pp. 50–60. Berlin: Springer-Verlag.
- Koehl, M. A. R., Powell, T. M. and Dairiki, G.** (1996). Effects of benthic organisms on mass transport at wave-swept rocky shores. *Eos Trans. Am. Geophys. Union* (Suppl.) **76**, OS69.
- Koehl, M. A. R., Powell, T. M. and Dobbins, E. L.** (1997). Effects of algal turf on mass transport and flow microhabitat of ascidians in a coral reef lagoon. *Proc. 8th Int. Coral Reef Symp.* **2**, 1087–1092.
- Koehl, M. A. R. and Wainwright, S. A.** (1977). Mechanical design of a giant kelp. *Limnol. Oceanogr.* **22**, 1067–1071.
- May, R. M., Roughgarden, J. and Levin, S. A.** (1989). (eds) *Perspectives in Ecological Theory*. Princeton, NJ: Princeton University Press.
- McMahon, T. A. and Bonner, J. T.** (1983). *On Size and Life*. New York: W. H. Freeman.
- Murdock, G. R. and Currey, J. D.** (1978). Strength and design of shells of the two ecologically distinct barnacles, *Balanus balanus* and *Semibalanus (Balanus) balinoides* (Cirripedia). *Biol. Bull.* **155**, 169–192.
- Nandakumar, K., Tanaka, M. and Kikuchi, T.** (1993). Interspecific competitions among fouling organisms in Tomioka Bay, Japan. *Mar. Ecol. Prog. Ser.* **94**, 43–50.
- Niklas, K. J.** (1992). *Plant Allometry: The Scaling of Form and Process*. Chicago: University of Chicago Press.
- Okamura, B.** (1984). The effects of ambient flow velocity, colony size and upstream colonies on the feeding success of Bryozoa. I. *Bugula stolonifera* (Ryland), an arborescent species. *J. Exp. Mar. Biol. Ecol.* **83**, 179–193.
- Okamura, B.** (1985). The effects of ambient flow velocity, colony size and upstream colonies on the feeding success of Bryozoa. II. *Conopeum reticulatum* (Linnaeus), an encrusting species. *J. Exp. Mar. Biol. Ecol.* **89**, 69–80.
- Peterson, J. A., Benson, J. A., Ngai, M., Morin, J. and Ow, C.** (1982). Scaling in tensile ‘skeletons’: structures with scale-independent length dimensions. *Science* **217**, 1267–1270.
- Santelices, B., Castilla, J. C., Cancino, J. and Schmiede, P.** (1980). Comparative ecology of *Lessonia nigrescens* and *Durvellia antarctica* (Phaeophyta) in Central Chile. *Mar. Biol.* **50**, 119–132.
- Schmidt-Nielsen, K.** (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.
- Schoener, T. W.** (1986). Mechanistic approaches to community ecology: A new reductionism. *Am. Zool.* **26**, 81–106.
- Tunncliffe, V.** (1980). Biological and physical processes affecting the survival of a stony coral. PhD dissertation, Yale University, New Haven, CT, USA.
- Wainwright, P. C. and Reilly, S. M.** (ed.) (1994). *Ecological Morphology: Integrative Organismal Biology*. Chicago: University of Chicago Press.
- Wake, D. B.** (1982). Functional and evolutionary morphology. *Perspect. Biol. Med.* **25**, 603–620.
- Woodley, J. D., Chornesky, E. A., Clifford, P. A., Jackson, J. C. B. J., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., et al.** (1981). Hurricane Allen’s impact on Jamaican coral reefs. *Science* **214**, 749–755.
- Worcester, S. E.** (1994). Adult rafting versus larval swimming: Dispersal and recruitment of a botryllid ascidian on eelgrass. *Mar. Biol.* **121**, 309–317.