

## How Do Benthic Organisms Withstand Moving Water?<sup>1</sup>

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**SYNOPSIS.** Many aquatic plants and animals spend part of their lives anchored to the substratum as water flows by. There are a number of mechanisms by which such sessile organisms can affect the magnitude of the flow-induced forces they encounter, as well as the distribution and magnitude of the mechanical stresses in their bodies produced by those forces. Furthermore, the mechanical properties of the skeletal tissues of such organisms affect how much they deform and whether or not they will break in response to flow-induced stresses. There are different mechanisms by which organisms can withstand the water flow characterizing a particular type of habitat. Biomechanics is a useful tool for studying how the performance of organisms depends on their structure. Biomechanical studies should be accompanied by knowledge of the natural history and ecology of the organisms in question if they are to lead to insights about how organisms work.

### INTRODUCTION

We who use an engineering approach in morphological studies are often accused of thinking that all organisms are beautifully designed for the functions they perform. In fact, biomechanics, like physiology, is just a way of trying to unravel *how* organisms work. I hope to illustrate in this paper that biomechanics is a useful experimental tool that enables morphologists to study in a quantitative and predictive way how the performance of organisms depends on their structure.

The task whose performance I will consider here is that of standing in one place—a task that may at first glance seem simple. Many plants and animals spend part of their lives anchored to the ground as the wind or water around them blows by. Such sessile organisms can be ripped up or broken by the moving fluid, and yet also depend on it to transport gases, nutrients, or food to them, to carry away wastes, and often to disperse their propagules. The structures of such organisms intrigue me because they should represent various compromises between maximizing and minimizing the effects of fluid flow.

I would like to illustrate some important physical facts of life for sessile organisms with examples from my research on benthic marine plants and animals. In exploring how these organisms withstand moving water, I will focus on several specific ques-

tions: How does the structure of an organism affect the water flow it encounters? the flow-induced forces it experiences? the deflection it undergoes? the likelihood that it will break? For the purposes of this paper I will describe in qualitative terms or in very simple equations some basic trends in how specific aspects of mechanical performance relate to certain parameters of body shape and size. However, since biomechanics is a quantitative science, I will include some references where those who care about such things can track down derivations or more rigorous engineering analyses.

### THE STRUCTURE OF AN ORGANISM CAN AFFECT THE WATER FLOW IT ENCOUNTERS

When water moves over a solid substratum, water in contact with the bottom does not slip relative to it, hence a boundary layer of water next to the substratum builds up in which a velocity gradient exists (see Jumars and Nowell, 1984). If an organism is flat enough, such as some encrusting bryozoans and sponges, or is small enough, such as some newly-settled larvae and benthic diatoms, it may be in a microhabitat characterized by lower water velocities than those of the mainstream flow. Just how short such an organism must be to hide within the boundary layer depends on the nature of the mainstream flow. For example, the faster the flow, the thinner the boundary layer. Since it takes some time after water starts moving over a surface for a boundary layer to build up, boundary layers can be especially thin on wave-swept shores hit by pulses of rapidly moving

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water. Similarly, the farther an organism sits from the leading edge of a rock (or coral plate or algal frond), the thicker the boundary layer in its vicinity. Quantitative descriptions of velocity gradients near solid surfaces (as can be found in Bird *et al.*, 1960; Batchelor, 1967; Schlichting, 1968) under different conditions can be used to estimate whether particular organisms hugging the substratum are likely to be in slower flow than mainstream.

Even large organisms at exposed sites can be in protected microhabitats if they sit in crevices or amongst other organisms. For example, the large sea anemones *Anthopleura xanthogrammica* that carpet the bottoms of wave-swept rocky surge channels encounter flow velocities much lower than mainstream because they take on a pancake-like posture and do not hold their tentacular crowns up above those of their neighbors. In contrast, solitary *A. xanthogrammica* at protected sites take on taller postures and extend into freestream flow; these tall "protected" animals encounter flow as fast as that seen by squat "exposed" animals (Koehl, 1977a). Furthermore, at protected sites short *A. elegantissima* that form mat-like clones encounter flow velocities about an order of magnitude lower than those seen by tall solitary *A. xanthogrammica* in their midst (Wainwright and Koehl, 1976). These anemones illustrate several points: 1) Flow microhabitats of particular organisms can be very different from the gross flow regime at a site. 2) Adjustment of height relative to neighbors (by active posture changes or by growth) is a way organisms can change their morphology to affect the velocity of water they encounter. 3) The packing together of organisms in aggregations, clones, or colonies can have a profound effect on the flow encountered by an individual (see also Chamberlain and Graus, 1975; Koehl, 1977d).

THE STRUCTURE OF AN ORGANISM  
AFFECTS THE MAGNITUDE OF THE  
FORCES IT EXPERIENCES IN  
MOVING WATER

Not only does the form of an organism affect the flow it encounters, but also the

magnitude of the forces it experiences in that flow. I will consider first the forces on organisms in steady flow (such as a tidal current) and will then discuss the forces on creatures exposed to unsteady flow (such as wave surge).

*Organisms in steady currents*

The force tending to push an organism downstream in a steady current is called drag (for details see Hoerner, 1965; Batchelor, 1967; Vogel, 1981). Because water resists being deformed in shear as it moves across the surface of an organism, the organism is subjected to a force, skin friction drag. Skin friction is essentially all you have to worry about when considering flow forces on very small or very flat encrusting organisms. However, most macroscopic plants and animals are subjected to another sort of drag as well that is generally greater in magnitude than skin friction: a turbulent wake forms on the downstream side of a large object in rapid flow, the net result of which is a greater pressure on the upstream side of the structure than on its downstream side. This pressure drag, or form drag, is proportional to velocity<sup>2</sup> and to some measure of an organism's area (which is proportional to length<sup>2</sup>), hence a small increase in flow rate or body length can lead to a large increase in drag. Any morphological feature of a macroscopic organism that reduces the size of the wake that forms behind it will reduce form drag.

We can conduct several sorts of experiments to investigate which morphological features of organisms affect the size of the wake and the drag they experience. We can alter the morphology of an organism by removing or adding specific structures (*e.g.*, Vogel, 1981), or we can change its orientation in a current (*e.g.*, Koehl, 1982a), and we can then measure the flow field around and drag force on it. We can also build physical models of organisms on which we can vary one morphological parameter at a time to see the effect on drag (*e.g.*, Koehl, 1977a). Furthermore, we can take advantage of "experiments" already performed for us by nature if we compare the flow around and drag on various species of plants or animals that differ from each other in

certain defined structural parameters (*e.g.*, Koehl, 1977*a, d*). Such experiments can be conducted in the field, on towing rigs, or in flumes. I would like to mention here just a few of the many examples of ways that the structure of an organism affects the magnitude of the drag it experiences.

If an organism takes on a shape or orientation that presents most of its surface area parallel rather than normal to the flow direction, wake size and drag are reduced (think of the force required to hold your hand parallel and then at right angles to a water current). A few of the many examples of stiff organisms (such as certain stony corals and limpets) with such drag-reducing shapes are cited in Wainwright and Koehl (1976) and Vogel (1981). Furthermore, flexible organisms (such as many seaweeds) are blown over into this drag-reducing orientation by water currents.

Many flexible organisms also collapse into more compact stream-lined shapes as flow velocities pick up. For example, my experiments with rigid and flexible models of the sea anemone *M. senile* showed that although the drag on both models was similar at low velocities, the drag on the flexible model (which deformed like an umbrella blown inside-out by the wind) was only two thirds of that on the rigid model in a  $1 \text{ m}\cdot\text{s}^{-1}$  current (Koehl, 1977*a*). This mechanism of reducing wake size and drag is discussed in some detail by Vogel (1984).

If an organism is flexible enough to be blown over sufficiently to lie near the substratum, drag can be reduced even further, as illustrated by the red alga *Gigartina exasperata*. These seaweeds, which look like Turkish towels, flop over near to the substratum in tidal currents. Although form drag is thereby much reduced, the alga still experiences skin friction drag. However, when a *G. exasperata* blade is near the substratum, only its upper surface is exposed to high flow velocities and therefore to high skin friction. The magnitude of the drag reduction provided by this mechanism is illustrated by comparing the drag on a *G. exasperata* next to a substratum with the drag on the same plant with no substratum nearby (Fig. 1) (Koehl and Mumford, unpublished data).

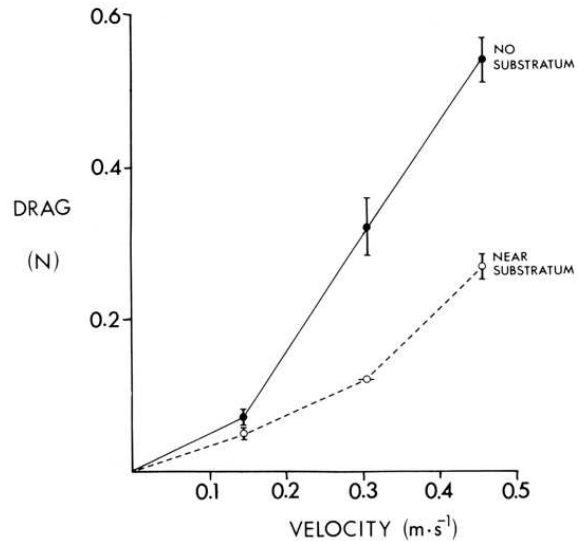


FIG. 1. Drag force measured on a *Gigartina exasperata* when next to and not next to a substratum. Water velocities were measured just upstream from the alga at the height of the blade when it was blown over. Error bars indicate one standard deviation (Koehl and Mumford, unpublished data).

#### *Organisms subjected to wave action*

The forces on organisms clinging to wave-swept shores are more complex than those on organisms in steady currents. Water in waves accelerates in different directions during the course of each wave (see Bascom, 1964; Wiegel, 1964; or Carstens, 1968, for descriptions of water motion in waves as they near the land, break, and rush up the shore). Organisms in such unsteady flow are subjected to acceleration reaction forces as well as drag forces (see Keulegan and Carpenter, 1958; Batchelor, 1967; Wiegel, 1964). The pressure differential on a body in a fluid subjected to gravity gives rise to a buoyant force on the body that is proportional to the mass of the fluid displaced by the body. Similarly, the pressure gradient on a sessile body in accelerating water gives rise to "virtual buoyancy," a force proportional to the mass of water the body displaces. Furthermore, when a swimming animal accelerates through a fluid, the animal's motion affects some volume of fluid, so the beast not only has to accelerate itself, but also the "added mass" of that fluid (Daniel, 1984). Similarly, when fluid accelerates past a stationary organism, this added mass con-

tributes to the force the organism experiences. The acceleration reaction force on a sessile organism in a wave is proportional to the organism's volume and the water's acceleration.

The force on a wave-swept plant or animal at any instant in time is the sum of the acceleration reaction and the drag at that instant (see Wiegel, 1964). Maximum drag occurs at a different time during a wave cycle than does maximum acceleration reaction, as illustrated in Figure 2 (drag is highest when velocity peaks whereas acceleration reaction is largest when the rate of change of velocity is greatest). Since form drag is proportional to some characteristic area ( $\propto \text{length}^2$ ) of an organism, whereas acceleration reaction is proportional to the creature's volume ( $\propto \text{length}^3$ ), we can predict that acceleration reaction will become increasingly important as wave-swept organisms increase in size. My calculations indicate that in surge channels sea anemones of the order of 10 cm wide should be subjected to acceleration reactions about six times greater than the drag they experience (Koehl, 1977a), although for smaller organisms such as limpets and barnacles, drag accounts for most of the force the animals experience (Denny, Daniel and Koehl, unpublished data). We can suggest that acceleration reaction imposes a physical upper limit on the sizes that organisms can become on wave-beaten shores (Denny, Daniel and Koehl, unpublished data; Denny, 1984).

There are some morphological features other than small size that can reduce the magnitude of the acceleration reaction a wave-swept organism must bear. One is to be of a shape that deflects as little water as possible (see Daniel, 1984); streamlined shapes and orientation of flat bodies parallel with the direction of water acceleration are acceleration-reaction-reducing features.

Flexibility is another feature that can reduce both the acceleration reaction and drag that organisms in waves must bear, as illustrated by large seaweeds. When a wave comes crashing in to shore, a long, flexible seaweed attached to the substratum moves *with the water* until it is strung out in the

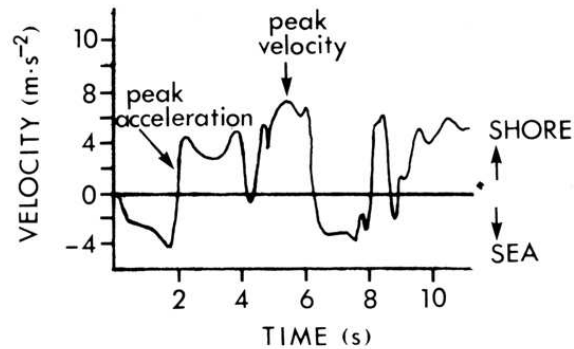


FIG. 2. Water velocities in the shoreward (+)-seaward (-) direction measured over intertidal rocks on a calm summer day on Tatoosh Island, Wa. The drag force on a rigid organism in such flow would be highest at times when velocity peaks, whereas acceleration reaction would be largest when the rate of change of velocity is greatest (*i.e.*, when the slope of such a tracing of velocity *vs.* time is steepest).

direction of flow; only then is there much water movement *relative to the plant* and does its thallus have to resist the significant flow forces. If an alga is long enough, the water that was rushing up the shore may be slowing down or starting to wash back down the shore before the plant is completely laid out with water moving past it. Therefore, flexibility in combination with great length provides a mechanism of avoiding bearing large flow forces in habitats subjected to oscillating flow. How long a flexible organism must be to play this avoidance game depends on both the velocity and duration of water movement in one direction. For example, I found that under non-storm conditions on Tatoosh Island, adult "sea palm" algae (*Postelsia palmaeformis*) were long enough to be moving with the water during periods of high acceleration, although they were sometimes strung out when peak velocities occurred. The longer algae *Lessoniopsis littoralis* at that site, however, were often still moving with the water when velocities were at their highest (Koehl, unpublished data). Note that for flexible organisms too short to totally avoid bearing high drag or acceleration reaction, the *durations* of these periods of high load are shorter than they would be if the organisms were rigid and could not move with the flow at all.



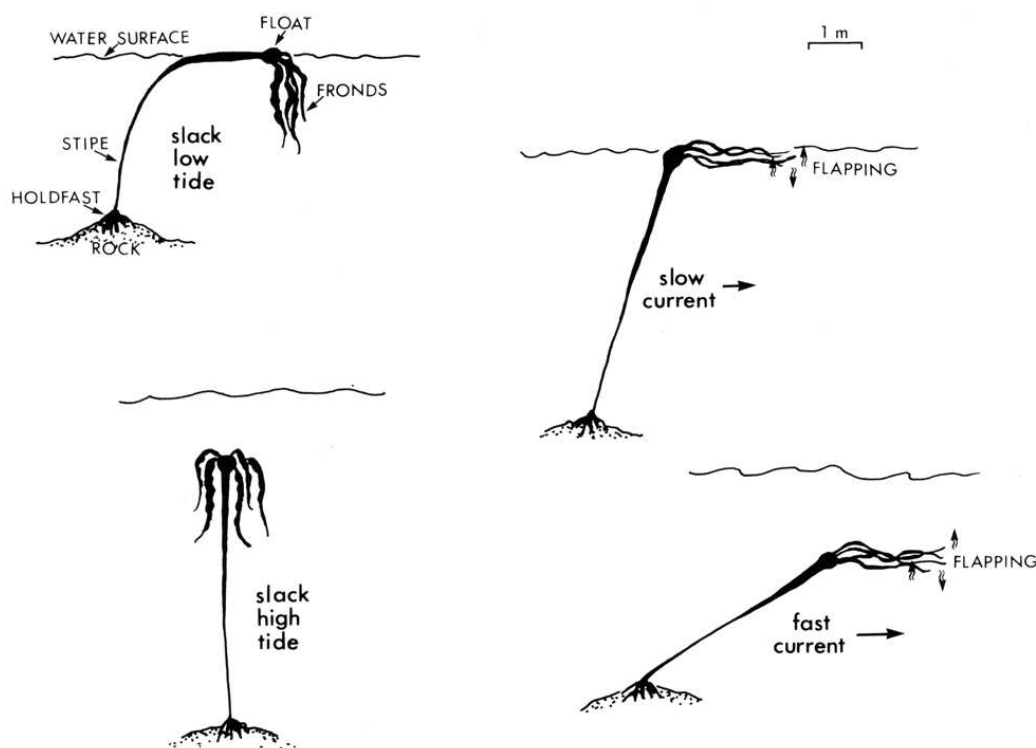


FIG. 3. Fronds of the giant bull kelp, *Nereocystis leutkeana*, are blown out parallel to the direction of water flow and flap like flags. Flapping is more pronounced for ruffled fronds from protected plants than for flat fronds from exposed plants.

*Morphological features that increase flow forces*

I should point out that flow-force reduction is not the only game in town. Many benthic organisms that make their living by extracting food or nutrients from the surrounding water have morphological features that increase how much they interfere with the water flow over them. Let me mention a few of the many examples.

Many passive suspension feeders are planar (e.g., some hydroid, gorgonian, and alcyonacean colonies). As you might expect, drag on such colonies is greater when their orientation is normal rather than parallel to the flow (e.g., Koehl, 1982a). However, most such organisms are at right angles to the flow in the field (Wainwright and Koehl, 1976). Planar organisms tend to be blown into this high-drag orientation because other orientations are not mechanically stable (Wainwright and Dillon, 1969). Furthermore, the animals catch

more plankton per time when oriented at right angles to the flow (Leversee, 1976).

The giant bull kelp of the Pacific Northwest, *Nereocystis leutkeana* (Fig. 3), provides another example of how sessile organisms can compromise between increasing and decreasing the effects of flow. Many algae have long, flat, floppy fronds. Although such fronds stream out parallel to the flow direction (reducing form drag), they also flap in the current like flags do in the wind (increasing form drag; see Hoerner, 1965). The fronds of *N. leutkeana* have ruffled edges in protected habitats but not at exposed sites. The drag per frond area is much higher for ruffled fronds because they flap with greater amplitude (thereby creating a bigger wake) than do unruffled fronds, and because they remain spread out laterally in currents rather than collapsing on top of each other into a nice streamlined shape the way unruffled fronds do (Koehl, unpublished data). Do these drag-increasing ruffles do anything for the algae?

Algal fronds pick up bicarbonate necessary for photosynthesis and release dissolved organics and oxygen by diffusion. The boundary layer of slowly-moving water on the surface of a frond can be thought of as a barrier across which diffusion takes place, hence the faster or more turbulent the flow across a frond (*i.e.*, the thinner the boundary layer), the greater its photosynthetic rate (up to some water-velocity saturation point, above which diffusion is no longer rate-limiting) (see Wheeler, 1980). *N. leutkeana* are at sub-saturation flow velocities for portions of the day (especially at protected sites), but flapping (which is more pronounced in ruffled than smooth fronds) stirs up the water around fronds and can nearly double photosynthetic rates for fronds in slow currents (Koehl and Alberte, unpublished data). We also found that if fronds stacked up right on top of each other (which is prevented by ruffles), the self-shading would reduce the photosynthetic rates of fronds underneath others.

These algae and suspension feeders are but a few examples of the many benthic organisms that interfere with and utilize the water moving past them, and hence have morphological designs that appear to be "poor" in terms of drag-reduction.

#### WHAT DO FLOW-INDUCED FORCES DO TO ORGANISMS?

In considering the job of standing in one place, I would like to focus on two aspects of performance: 1) deformation, and 2) breakage.

How much organisms of particular morphologies will deflect in moving water can be predicted from basic engineering principles. However, whether resistance to deflection is a "good" or "bad" feature for a plant or animal can only be determined if one knows about the habitat and ecological interactions of the organism. For example, must an organism be able to hold its photosynthesizing structures rigidly over those of its neighbors to outcompete them? Must it be able to hold a net in a fixed configuration in a current to catch its dinner? Conversely, can an organism survive winter storms by deflecting when waves hit? Can a flexible organism fling off would-be

predators, or sweep the surrounding substratum clear of potential competitors as it flails around in the crashing surf?

Similarly, the probability that organisms of particular morphologies will break when living in defined habitats can be estimated from engineering principles (*e.g.*, Denny, Daniel and Koehl, unpublished data), but whether or not such breakage is "bad" depends on the habitat and life history of the organisms. Does breakage equal death for an individual? Is breakage a mechanism of asexual reproduction? Can an organism complete its growth and production of propagules before the onset of seasonally-predictable heavy wave action?

To analyze how the morphology of an organism determines its deformability and breakability, we need to explore how the shape of an organism affects the magnitude of the stresses in its body (stress is a force divided by the cross-sectional area of material bearing that load). We also need to consider how the mechanical properties of the tissues and skeletal materials of the organism determines their response to those stresses. The mechanical behavior of the materials of which a plant or animal's body is made depends in turn on the microscopic and molecular structure of those materials. Although I will not deal in this paper with how morphology at the microscopic or molecular levels of organization relates to mechanical performance, numerous examples can be found in Wainwright *et al.* (1976), Vincent and Currey (1980), and Vincent (1982).

#### STRESSES DEPEND ON BODY SHAPE

There are a number of ways in which sessile organisms can deform in flowing water, as diagrammed in Figure 4. This figure also includes a few simple equations that point out some of the basic trends to keep in mind about how stress depends on the shape of an organism. (For stress analyses of various types of structures under different loading regimes, see for example, Timoshenko and Gere, 1972; or Faupel and Fisher, 1981.) Obviously, since the magnitude of the stress depends in part on the magnitude of the load ("F" in Fig. 4) on the organism, any morphological feature that reduces flow forces should also

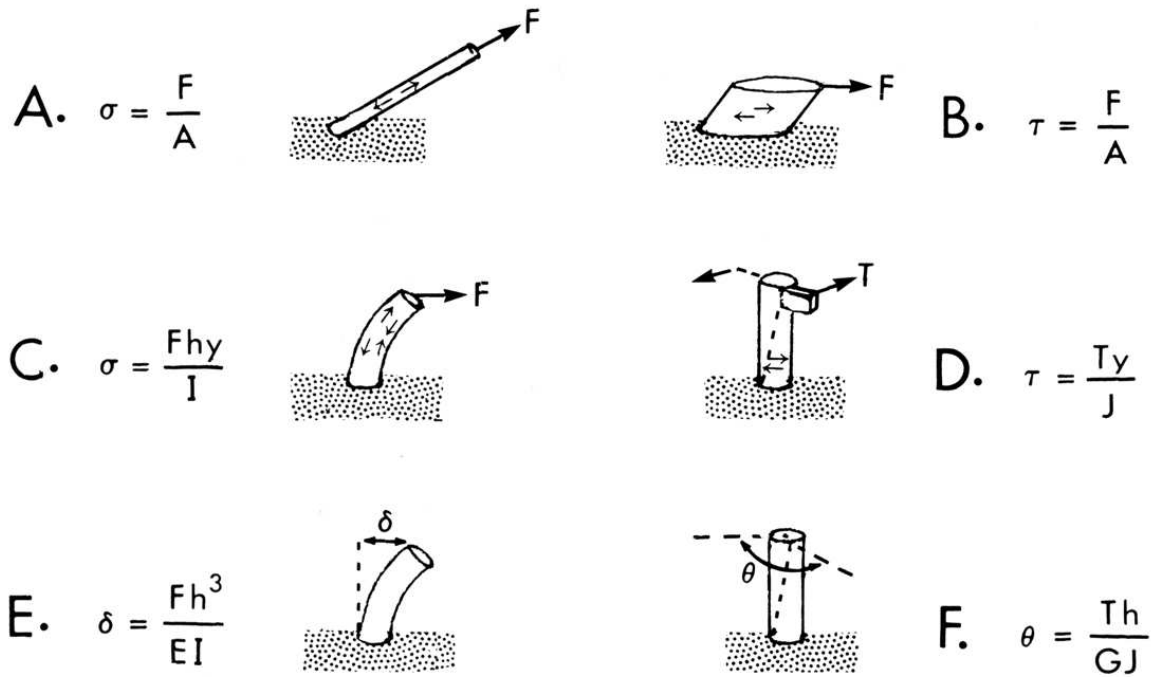


FIG. 4. Diagrams of some of the ways a sessile organism can deform when bearing a load such as a flow-induced force. Heavy arrows indicate (in A-D) the direction of force application, and fine arrows indicate the deformation of the organism's tissues. Symbols:  $\sigma$  = tensile stress;  $\tau$  = shear stress;  $F$  = force or load applied to the organism,  $T$  = torque applied to the organism;  $A$  = cross-sectional area of the organism;  $h$  = distance from the free end of an organism to a bit of tissue (in C), or height of the organism (in E and F);  $y$  = distance along the radius of an organism from the axis of bending or rotation to a bit of tissue (in C and D), or radius of the organism (in E and F);  $I$  = second moment of area;  $J$  = polar second moment of area;  $\delta$  = linear deflection of the free end of a bent organism;  $\theta$  = angular deflection of the free end of a twisted organism;  $E$  = tensile elastic modulus of the material of which the organism is made;  $G$  = shear elastic modulus of the material. A. Stress in an organism in tension. B. Stress in an organism in shear. C. Stress in an organism in bending. One side of the body is stretched and the other is compressed. D. Stress in an organism in torsion. E. Deflection of an organism in bending. F. Deflection of an organism in torsion. How far an organism deflects (E and F) depends on size and shape in two ways: The magnitude of stresses depend on height and width of the organism, and the summation of all the deflections of all the little sections of an organism's body results in a bigger overall deflection of the free end of the organism if more such deflections are summed, *i.e.*, if the organism is taller.

reduce stress. However, body shape affects stress in other ways as well.

If an organism is bent by flowing water, the tensile stress (" $\sigma$ " in Fig. 4) in a small bit of tissue is proportional to the distance of that bit of tissue from the free end of the organism (" $h$ " in Fig. 4). Hence, stress is greatest in tissues near the attached end of the organism (if it is uniform in cross-sectional size and shape along its length), and the maximum stress is greater in a tall organism than in a short one of the same cross-section and bearing the same load. Similarly, if an organism is twisted the shear stress (" $\tau$ " in Fig. 4) is great if the torque (" $T$ ") is high. Since torque is a force times a moment arm (the distance from the axis

of rotation at which the force is acting), the farther one side of an organism's body sticks out from its axis of rotation than the other side sticks out, or the greater the flow force on one side relative to the other, the greater the shear stresses in the organism.

If an organism is bent or twisted, stresses are greatest in tissues far from the axis of bending or twisting, *i.e.*, at the periphery of the body (see " $x$ " in Fig. 4). Furthermore, for a bent or twisted organism, the magnitudes of the stresses are inversely proportional to the second moment of area (" $I$ " in Fig. 4) or polar second moment of area (" $J$ "), respectively.  $I$  and  $J$  are measures of the distribution of material around the axis of bending or twisting, and are

roughly proportional to the width of the organism raised to the fourth power. Hence, a small decrease in width can lead to a large increase in stress for a given load. Think about the huge effect that a grazer's bite can have when taken out of the stalk of a sessile organism!

In contrast, if an organism is pulled or sheared by given load, the tensile or shear stress in its tissues is inversely proportional to its cross-sectional area ("A" in Fig. 4), but cross-sectional shape does not make much difference.

Consider the example of two species of intertidal seaweeds that are abundant along wave-swept rocky shores of Chile: *Lessonia nigrescens* and *Durvillea antarctica*. Field measurements indicate that both species encounter the same range of flow forces (Koehl, 1979), but they differ in their response. *L. nigrescens* stipes, which are wide near their bases and relatively stiff, are bent in flowing water. In contrast, *D. antarctica*, which have flexible joints at the bases of their stipes, flop over and are pulled by moving water. Calculations indicate that stresses in a bent *L. nigrescens* stipe are roughly 800 times greater than in a pulled *D. antarctica* stipe of the same dimensions and bearing the same load (Koehl, 1982b). These seaweeds illustrate a general principle about organisms bearing loads: stresses are lower if an organism bears a given load in tension than in bending.

Consider now the example of the surge-swept sea anemones mentioned earlier, *A. xanthogrammica*, and the subtidal sea anemones, *Metridium senile*. Although the tidal currents to which *M. senile* are subjected are slower than the surge encountered by *A. xanthogrammica*, the flow forces on an individual of either species are roughly the same because *A. xanthogrammica* has a more drag-minimizing shape (Koehl, 1977a). Nonetheless, maximum stresses in the tall, slim *M. senile* are about 45 times greater than in the short, wide *A. xanthogrammica* (Koehl, 1977b). These anemones illustrate another general principle about the design of organisms: tall, slim shapes are stress-increasing whereas short, wide shapes are stress-decreasing. Note in the example of these sea anemones that stresses in the

"protected" *M. senile* are much greater than in the "exposed" *A. xanthogrammica*. It is a good idea to do stress analyses before claiming that one habitat is more mechanically "stressful" than another!

#### DEFLECTION

How far an organism deflects in response to flowing water depends on its shape and on the stiffness of its tissues. For example, for a given load tall organisms bend or twist more than short ones, and slim ones more than wide ones made of the same material (Fig. 4). The E and G in the denominators of the deflection equations in Figure 4 represent the tensile and shear elastic moduli respectively of the tissues of the organisms and are basically a measure of their stiffness or resistance to deformation. If a tissue is pulled and the force per area (stress) with which it resists extension is plotted against extension (expressed as the ratio of extended length to original length), the slope of such a curve is the tensile elastic modulus (E). (Analogous tests can be done in shear to measure G.) Stiff materials, which pull back harder at a given extension than do stretchy materials, have steeper curves (compare curves "a" and "b" in Fig. 5). An organism built of material of low elastic modulus will deform more under a given load than will an organism of the same dimensions whose tissues have a higher elastic modulus.

At this point I should issue a warning about some biological materials. The curves "a" and "b" in Figure 5 were made for pieces of body-wall connective tissue (mesoglea) from one individual *M. senile*, a sea anemone mentioned above; specimen "a" was pulled quickly and specimen "b" was pulled slowly. For tissues such as this whose stiffness depends on the rate at which they are deformed, one must have an estimate of their deformation rate in the field to predict the performance of the organism. Knowing the flow-induced forces and the morphology of an organism, one can estimate the magnitude of the stresses in the organism's tissues. One can then subject isolated pieces of tissue to stresses that simulate those in the field under different conditions, and can measure tissue exten-



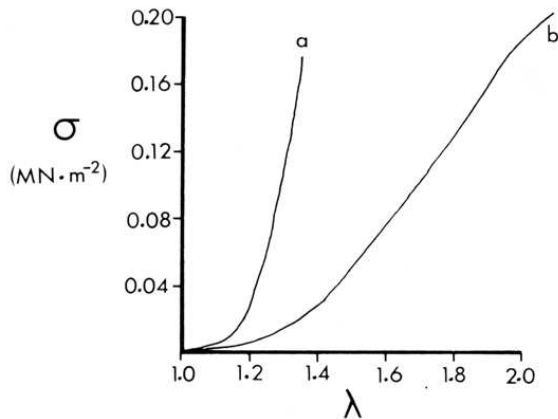


FIG. 5. Stress ( $\sigma$ ) in *M. senile* body wall connective tissue pulled to different extension ( $\lambda$  = ratio of extended length of specimen to its original unpulled length). Specimen "a" was pulled at a rate of  $0.05 \text{ s}^{-1}$  (extension rate is expressed as the ratio of the change in length to the original length of the specimen per second) whereas specimen "b" was pulled at a rate of  $0.005 \text{ s}^{-1}$  (redrawn from Koehl, 1977b).

sion. For sea anemone mesoglea, I found that the greater the stress, the greater the rate of extension. That is not surprising, but it points out a non-intuitive feature of a number of sessile organisms whose tissues are extension-rate-dependent: body shape determines the magnitude of stresses in the tissues, and the magnitude of stress determines deformation rate, which in turn affects the stiffness of the tissues (*i.e.*, body shape can affect how stiff an organism's tissues are!) (Koehl, 1977b).

Mesoglea from sea anemones provides an example of another way we should consider the time scale of how a tissue is used in the body of an organism. A sea anemone has a hydrostatic skeleton; mesoglea forms the bulk of the load-bearing wall of such "water balloons" (as described, for example, in Wainwright *et al.*, 1976). Results of a creep test (in which a constant stress is applied to a tissue and its extension with time is measured) are given for *M. senile* mesoglea (curve "a") in Figure 6. Note that at short times (of the order of seconds to minutes) the material does not deform much. This time scale corresponds to the time scale of muscular shape changes by the animal. To the anemone's muscles, the mesogleal wall of the hydrostatic skeleton

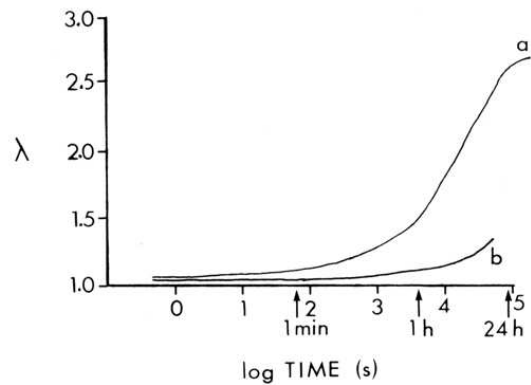


FIG. 6. Results of creep tests on *M. senile* mesoglea ("a") and *A. xanthogrammica* mesoglea ("b"). A constant stress was applied to each specimen and its extension ( $\lambda$  = ratio of extended length of specimen to its original length) was measured with time (plotted on a logarithmic scale here) (redrawn from Koehl, 1977c; curve "a" is also similar to results reported by Alexander, 1962).

is reasonably stiff, hence a local contraction will lead to a shape change or movement rather than an aneurism. Over a time scale of the order of a few hours, the mesoglea deforms more. This time scale corresponds to that over which the anemone is bent by tidal currents (Koehl, 1977a). (When *M. senile* are bent over by currents, their filter-feeding oral disks are passively oriented at right angles to the flow direction.) After very long times (of the order of 12 to 24 hr), the mesoglea undergoes huge extensions (which are reversible if the load is removed), even when subjected to small stresses. This corresponds to the time scale of inflation of the animal to a very expanded configuration (see Batham and Pantin, 1950). The inflation is carried out by a weak ciliary pump that can generate only very low internal pressures. Thus, to the animal's muscles, the mesoglea is reasonably stiff, to the tidal currents it is more deformable, and to the ciliary pump it is extremely stretchy. Therefore, how stiff I claim *M. senile* mesoglea is depends on the time-scale of the function I am considering. Note, in contrast, that the mesoglea of an *A. xanthogrammica* (Fig. 6, curve "b") does not extend much, even after many hours of bearing a load. These anemones can be hit by waves all day long without getting stretched out (Koehl, 1977c). These

anemone tissues are just two of many examples of how the mechanical performance of an organism depends on morphological features at the molecular and microscopic levels of organization as well as at the gross morphological level (for details see Alexander, 1962; Gosline, 1971a, b; Koehl, 1977c).

Another example of the importance of the time scale of loading to the behavior of tissues is provided by the spicule-reinforced connective tissues of fleshy colonies of alcyonacean "soft corals." On a short time scale, heavily-spiculated tissues are stiffer than lightly-spiculated ones, but over long time scales they show time-dependent stress-softening and become much stretchier than lightly-spiculated tissues (Koehl, 1982a). To predict the performance of such spiculated animals, we must know not only the distribution of spicules in the body, but also the time scales of the loads the tissues bear.

#### BREAKAGE

The second aspect of the performance of sessile organisms that I would like to consider is whether or not they break when subjected to tidal currents or crashing waves. Consider the example of the two species of Chilean algae mentioned above, *L. nigrescens* and *D. antarctica*. *L. nigrescens* stipe material is stiffer, and it breaks at a higher stress (*i.e.*, is stronger) than does *D. antarctica* stipe material (Fig. 7). However, *D. antarctica* stipe tissue extends more before breaking than that of *L. nigrescens*. The area under each stress-extension curve is a measure of the amount of work per volume of tissue that a wave (or a biologist) must perform on the tissue to break it. The bigger the area, the greater the work-to-break, and the tougher the material. In the case of these two seaweeds, the stipes do not differ significantly from each other in toughness (Koehl, 1979). These algae illustrate that very different strategies can render an organism tough: 1) being stiff and strong (but not too stiff; see Currey, 1984), or 2) being extremely extensible, even if not strong. Note that organisms using the strength approach should be less likely to break than organisms using the extensi-

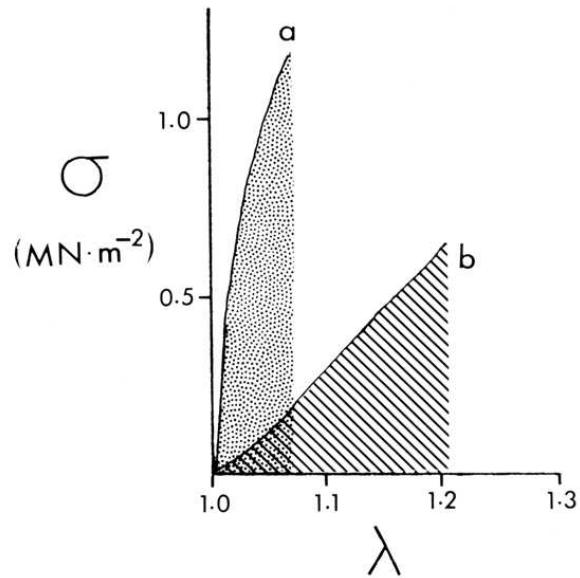


FIG. 7. Stress ( $\sigma$ ) in the stipe material of *L. nigrescens* and *D. antarctica* pulled to different extensions ( $\lambda$  = ratio of extended length to original length of the specimen) until each broke. The area under each curve represents the work per volume of tissue required to break each specimen.

bility strategy in habitats where high loads are applied for a long enough time to stretch the extensible creatures out to their breaking lengths. In such situations a stress high enough to break an extensible, weak organism might be too low to break a stiff, strong one. Conversely, extensible organisms are better "shock-absorbers" than stiff organisms. Stretchy tissues deform before they transfer the full load hitting an organism to the glue sticking it to the rock (Denny, Daniel and Koehl, unpublished data).

Are there ecological correlates of these two mechanical strategies at the tissue level? The work of Santileces *et al.* (1981) on the Chilean seaweeds indicates that the extensible *D. antarctica* are faster-growing and produce spores sooner after settlement than do the strong *L. nigrescens*, but suffer more breakage during winter storms and thus tend to be shorter-lived than *L. nigrescens*. *D. antarctica* propagules settle year round whenever bare space becomes available on the rock, whereas settlement of *L. nigrescens* is seasonal. Both Santileces *et al.* (1981) and I (Koehl, unpublished data) found that most of the breakage that *L.*

TABLE 1. Toughness<sup>a</sup> of some biological and man-made materials.

0.01-0.1	0.1-1	1-10	10-100
Stony coral skeleton	<i>N. leutkeana</i> stipe <sup>b</sup>	Chitin	<i>L. nigrescens</i> stipe <sup>c</sup>
Mollusk shell	Sea whip axis	Resilin	<i>D. antarctica</i> stipe <sup>c</sup>
Crab carapace	Echnoid spine	Keratin	Cellulose
Balsa wood	Bone	Steel	Tendon
Concrete	Insect cuticle		Silk
	Oak wood		Nylon
	Cast iron		

<sup>a</sup> Work to break per volume of material, MJ·m<sup>-3</sup>.

<sup>b</sup> From Koehl and Wainwright (1977).

<sup>c</sup> From Koehl (1979); all other values from Wainwright *et al.* (1976).

*nigrescens* eventually suffers is due to the action of grazers on and borers in its tissues (remember, bites and bore-holes reduce second moment of area, and therefore lead to large increases in stress for a given load on a plant). *L. nigrescens*, however, have the ability to regrow after being pruned by grazing and wave action, whereas *D. antarctica* do not (Santelices *et al.*, 1981). Whether or not most organisms that are tough by being extensible show the life history characteristics of a weedy opportunist, as *D. antarctica* does, and most organisms that are tough by being strong show the characteristics of long-term space-holders as *L. nigrescens* does, remains to be seen. We need to know about *both* the biomechanics and ecology of many more organisms before we can see whether such patterns exist.

Table 1 shows a listing by order of magnitude of the toughnesses of various biological and man-made materials. Note that stipe tissues from *L. nigrescens* and *D. antarctica* are right up there with the best of them. If we look at the opposite end of the spectrum at the breakable materials, we find both very brittle, stiff materials like coral skeletal material, and very weak, stretchy materials like *N. leutkeana* stipe tissue. How do brittle corals and weak seaweeds survive at wave- or current-swept sites?

The Caribbean stony coral *Acropora cervicornis* forms long, slim branches (a stress-increasing shape) supported by brittle skeletal material. We can predict that these corals would break in rapid water flow, yet we find that they thrive on wave-swept

forereefs. *A. cervicornis* do often break, but the broken-off pieces survive and grow. Such "programmed breakage" and growth appears to be the main mechanism of asexual reproduction and dispersal of *A. cervicornis* colonies (Tunnecliffe, 1980) as well as of a number of other species of coral (Highsmith, 1982). Hence breakability is not necessarily a "bad" feature for organisms that can regrow. Furthermore, when bits of an organism or colony break off, the flow forces on the whole structure can be reduced, hence partial breakage can prevent total destruction (*e.g.*, Black, 1976). We should expect such breakage to occur at skinny regions of the body (high stress regions), or at localized regions of material with a low work-to-break and/or low strength.

Other more robust corals do not routinely break like *A. cervicornis*, but do suffer damage during catastrophic events like hurricanes. As you would predict on mechanical terms, more of the tall, slim branching corals were broken when Hurricane Allen hit Jamaican coral reefs than were mound-like forms (Woodley *et al.*, 1981). You should also not be surprised that we found many tough, flexible gorgonian sea fans and whips still in place after the storm. However, many corals and gorgonians that did not break had their living tissue scraped off by the sand and rubble carried in the water during the hurricane. This illustrates that managing not to break is not all there is to survival of mechanically stressful events.

Now consider organisms that are weak (*i.e.*, break at a low stress), but are very

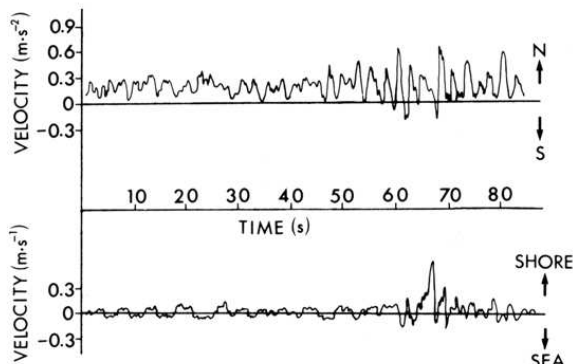


FIG. 8. Water velocities in the shoreward (+)–seaward (–) directions (this is the flow associated with waves) and north (+)–south (–) alongshore directions (this is the flow associated with the tidal current) measured at frond height in a *N. leutkeana* bed near San Juan Island, Wa.

extensible, such as the bull kelp *N. leutkeana*. On mechanical terms we might predict that organisms made of such materials could survive in current-swept habitats if 1) they are not subjected to large loads for times long enough to extend them to the breaking point (*i.e.*, they occur at sites where high flow velocities are of short duration), and 2) their material is resilient enough to bounce back to its unstretched length before the next wave hits.

*N. leutkeana* occurs at sites exposed to tidal or along shore currents (which can be quite rapid); however, near the water surface (where the fronds, which are responsible for most of the drag on the plant, are held) waves are superimposed on those currents (Koehl, unpublished data). In Figure 8 water velocity encountered by *N. leutkeana* fronds is plotted against time. Note that although peak velocities are high, they only last a fraction of a second. Furthermore, tensile free-vibration tests (Nielson, 1963) indicate that *N. leutkeana* stipes are extremely resilient (Koehl, 1982*b*). Moreover, *N. leutkeana* are rapidly-growing annual plants that generally release their spores before they are ripped up and cast ashore by autumn and winter storms.

One important aspect of the breakage of sessile organisms about which very little is known is fatigue fracture. When some materials are subjected to repeated stresses that are too low to break them initially, the

materials eventually fracture. (Anyone who has broken a coat hanger by bending it back and forth repeatedly is familiar with this phenomenon.) How do organisms hit over and over again by waves avoid fatigue fracture, and what role does growth and repair play?

#### SUMMARY

We can use basic engineering principles to analyze how the mechanical performance of organisms depends on their structure. Some basics of the design of benthic marine organisms that stand in one place include:

1. The shape and behavior of an organism can affect the flow the organism encounters. Plants and animals can spatially avoid rapid flow at current-swept sites if they are small or flat enough, if they aggregate, or if they adjust their height relative to surrounding objects. Organisms can also temporally avoid high velocities and accelerations, for example, at wave-swept sites by being flexible, or at seasonally-varying sites by growing and reproducing before the stormy season hits.

2. For macroscopic organisms, any feature that reduces wake size reduces drag. Such features include flexibility and shapes that present most of a body's surface area parallel to the flow direction. However, many current-swept organisms have drag-increasing features.

3. The morphological/mechanical features that permit organisms to survive in an unsteady flow regime (as encountered on wave-beaten shores) are not necessarily effective in a steady flow regime, and vice versa.

4. Body shape not only affects the magnitude of flow-induced forces, but also determines the magnitude and distribution of stresses in an organism subjected to a given load. Body size and tissue stiffness determine how much deflection will occur in response to those stresses. An organism (or a region of an organism) will be flexible if second moment of area (a shape parameter) and/or elastic modulus (a material property) are low.

5. The time scale of loading can affect the mechanical behavior of an organism.



It is important to know the deformation rates and the durations of loads on organisms in nature if one is to predict their mechanical performance.

6. An organism's tissues can be tough by being stiff and strong, or by being very extensible, even if not strong. However, many plants and animals, even on wave-beaten shores, are not tough.

#### CONCLUSIONS

I hope I have convinced you that standing in one place is not as simple as it may at first seem, and that there are many different ways of doing the same mechanical task. Furthermore, many organisms with "bad" mechanical designs can thrive at wave- or current-swept sites because of their particular life history strategies.

The message I would like to get across to biomechanicians is that, if our research is to tell us how organisms work, it is very important that we know the natural history (*e.g.*, the microhabitats, the time scales of activities and load-bearing, the reproductive strategies, the ecological roles) of the organisms whose functional morphology we are studying.

I have a different message for ecologists and evolutionary biologists: An engineering approach is a powerful tool allowing us to study in an experimental, quantitative, and predictive way how specific aspects of the performance of organisms relate to their structure. My aim is not to show that organisms are optimally designed to do what they do, but rather to study *how* they do what they do.

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