The Interaction of Moving Water and Sessile Organisms

A host of marine organisms live attached to the bottom close to the shore. They show a remarkable array of adaptations to the forces exerted by strong currents and crashing waves

by M. A. R. Koehl

Anyone walking along an exposed rocky seacoast at low tide may notice that a remarkable number and variety of plants and animals live attached to the bottom and that they are often battered by waves. Such sessile organisms are at risk of being ripped away by the moving water, and yet they depend on the water to bring them nutrients, to carry off their wastes and often to disperse their offspring to new locations. How do they manage?

What one learns on examining sessile plants and animals closely, as I have been doing along the Pacific coast of North and South America and on Caribbean coral reefs, is that the organisms embody diverse compromises between maximizing and minimizing the effects of flowing water. Organisms living in a slow flow often have features that compensate for the lack of transport by moving water; for example, they can create their own feeding currents or tolerate low levels of oxygen. Similarly, organisms living in a fast flow often have features that enhance their ability to withstand and utilize the water rushing past them. The features that enable sessile organisms to stand in one place are more varied than one might expect.

A number of questions confront the investigator who wants to explore how a sessile organism deals mechanically with moving water. How does the structure of the organism affect the flow of water past it and the flow-induced forces on it? How does the organism's shape determine the stress on its tissues when it is subjected to flow forces? (Stress is the force or load per cross-sectional area of the material bearing the load.) How does the structural material of an organism affect the way it deforms or breaks in response to flow-induced stresses?

Sessile marine organisms live in several basic types of flow. There is a major distinction between intertidal and subtidal habitats, that is, the habitats between the low- and high-tide lines and the habitats seaward of the low-tide line. An intertidal plant or animal in a place where waves break on an exposed coast is subjected to a fast, turbulent flow. I have measured the flow over such organisms and found the velocity to be highest during the shoreward surge and seaward backwash just after a wave has broken.

For organisms living on the bottom in the high subtidal zone of a wave-swept shore the back-and-forth flow they encounter as waves pass overhead is slower. (Remember that the position of an organism with respect to the breaking waves, and hence the type of flow it encounters, changes as the tide rises and falls.) If an organism lives deeper than half the distance between the crests of successive waves passing overhead, it does not "feel" the waves. These organisms, as well as those living in protected bays and sounds, are exposed instead to steady currents or to the steady but periodically reversing currents of the tides.

What I have described so far could be called macrohabitats of flow. Each macrohabitat contains local microhabitats where the flow is different. To study a microhabitat one must take into account a basic feature of a fluid flowing over a solid surface: the flow is slowest nearest the surface. This layer of slowly moving fluid is known as the boundary layer; the slower the flow is or the farther one looks behind the leading edge of an object, the thicker the boundary layer is. Extremely small organisms (newly settled larvae and bottom-dwelling unicellular plants and animals) and flat encrusting organisms (crustose algae and some bryozoans, or moss animals) live in the boundary layer. The flow microhabitat of a short organism can be quite different from the mainstream flow over the area where it lives. Furthermore, the marine environment is generally not flat and smooth; the bumps and crevices and even the other organisms around a large plant or animal can markedly alter the flow past it.

Sea anemones of the genus *Anthopleura* provide good examples of animals living in surprising flow microhabitats. They are common on rocky shores from California to British Columbia. The great green anemone (*A. xanthogrammica*) carpets the bottom of intertidal surge channels at particularly exposed sites. Adhering to the bottom in the low intertidal zone, they live by ingesting mussels and sea urchins knocked down onto them by waves.

I have measured flows in the mainstream of such surge channels and flows down where the anemones are. In the mainstream the flow can be up to five meters per second on nonstormy days; at the tentacles of the anemones it is much slower. Great green anemones are as much as 20 centimeters (eight inches) across, but in an exposed channel they are pancake-shaped, with an average height above the rock of 2.5 centimeters (an inch). In other words, they avoid the fast flow by hunkering down.

Some great green anemones can also be found at more protected sites where the brunt of the waves is absorbed by rocks to seaward. In such a habitat the anemones stand at an average height of seven centimeters. Even though the mainstream flow at protected sites is much slower than it is in surge channels, the taller anemones stick up into the flow and therefore encounter velocities equal to or greater than those met by their short relatives in exposed channels.

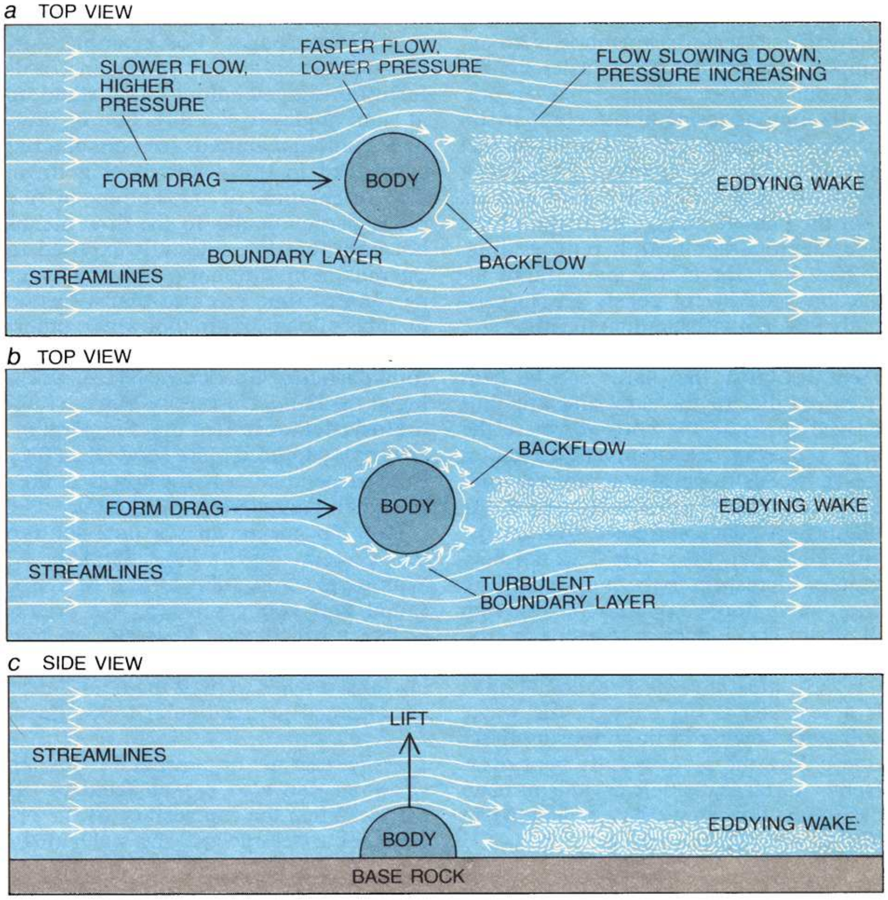
Great green anemones at less exposed sites are often found side by side with smaller anemones of the species *Anthopleura elegantissima,* the aggregating anemones, which reproduce by splitting in two longitudinally so that they eventually cover the rocks with matlike clones. I found that the water passing these small, closely packed anemones traveled at only a tenth of the speed of

BELT OF SEAWEED along the rocky coast of central and southern Chile is exposed to heavy seas that impose strong forces on the tissues of a plant. The force is applied in one direction as a wave breaks and in the other direction as the water from the broken wave runs seaward. This seaweed is *Lessonia nigrescens,* which responds to the forces by bending with the flow. A companion seaweed in the belt, *Durvillea antarctica,* is pulled by the flow so that it lies more or less parallel to the sea bottom. The maximum stress in a stipe, or stem, of a seaweed pulled by the flow, as *D. antarctica* is, is considerably less than that in a stipe of a seaweed that bends, as *L. nigrescens* does.

GREAT GREEN ANEMONES, *Anthopleura xanthogrammica,* carpet the bottom of surge channels on exposed rocky shores. These anemones were photographed in such a channel on Tatoosh Island off the northwest tip of the state of Washington. In a surge channel the great green anemones, being sessile, cope with the strong flow by hunkering down close to the bottom, where the flow is slower than the mainstream flow. In a more protected place, where much of the force is absorbed by seaward rocks, *A. xanthogrammica* stands taller.

the water passing a large, solitary great green anemone in their midst. The contrast indicates how different the flow microhabitats of organisms living side by side can be.

Many colonial marine animals, such as corals and hydroids, secrete a skeleton that supports the individuals of the colony (the polyps). The animals create the terrain on which they live and thereby modify their own flow environments. In order to visualize the flow around the branches of corals and models of corals John Chamberlain of Brooklyn College of the City University of New York and Richard Graus of Cleveland State University put dye in water. As one might expect, they found that the diameter, spacing and arrangement of the branches all affect the speed and direction of water movement within the colony. More surprisingly, they found that quite different colony configurations can give rise to the same pattern of flow over the polyps. The polyps of gorgonian sea whips and sea fans occupy flexible skeletons that sway back and forth as waves pass over them. Since the skeleton moves with the water, the flow with respect to the polyp can be low even though the colony lashes about in a habitat of heavy surge.



FLOW FORCES on a sessile marine organism are depicted schematically. As the velocity increases along a streamline (the path traveled by a particle of fluid) the pressure decreases, and vice versa. When water flows around the widest section of a body (*a*), its speed increases and the pressure it exerts on the surface of the body decreases. Beyond the widest section the fluid slows and the pressure rises. Viscosity causes fluid particles in the boundary layer (closest to the body) to lose momentum as they pass the body. When the flow over the body is fast enough and the body is large enough, this viscous retardation will stop the downstream progress of the water in the boundary layer, which may then be pushed upstream by the increasing pressure of the decelerating fluid around it. Behind the body a wake of eddying fluid separates from the mainstream flow, so that the pressure there is lower than it is at the front. This net downstream pressure is termed form drag. If the fluid is moving fast enough with respect to the body (*b*), the boundary layer becomes turbulent and momentum is transferred to it from the mainstream flow, giving rise to a smaller wake and less form drag. As the fluid moves faster across the top or one side of a body (*c*) the low pressure there tends to suck the body upward or sideways. The force is called lift but is not always upward; it can be at any right angle to the flow.

The shape, size and texture of a sessile organism affect the magnitude of the mechanical forces exerted on it when water flows across it. Drag forces, which tend to push an organism downstream, are due to the viscosity of water: the tendency of water molecules to resist sliding past one another. Water sticks to solid surfaces, including the surfaces of organisms, and a boundary layer of water around an organism is subjected to shearing forces as the flow passes by. Since water is viscous and resists being sheared, the result for the organism is skin-friction drag. The magnitude of the drag is proportional to the velocity of the flow and the length of the object and therefore gets larger as organisms increase in size or encounter faster flows.

The drag on small organisms in a slow flow is due mainly to skin friction. Large organisms in a fast flow are affected by an additional drag, called form drag, that is generally much stronger than skin friction. On the downstream side of an organism a turbulent wake forms. The pressure on the upstream side is greater than that on the downstream side, and so the organism tends to be pushed downstream. Any feature of an organism that reduces the size of the wake reduces form drag. The magnitude of form drag is proportional to the area of the body and the square of the velocity, and so a fairly small increase in length or velocity can lead to a comparatively large increase in form drag.

Several approaches are available to the investigator seeking to study how an organism's shape, surface texture and flexibility affect drag forces. One can compare the drag forces and the patterns of flow around similar organisms that differ in particular characteristics. One can also make models of the organisms, modifying various features in order to measure their effect on drag. Sessile organisms or models are attached to force transducers on the shore or in a flow tank or a towing rig, where the velocity of flow is controlled. Patterns of flow around the bodies are visualized with dye or marker particles or are measured by small electronic probes.

If a large organism has most of its surface parallel to the flow rather than at a right angle to it, it will create a smaller wake and therefore reduce form drag. This simple way of reducing drag is well illustrated by the forces on two species of large sea anemone: the squat great green anemone I have mentioned and the tall, fluffy species *Metridium senile,* which has a large, fluted crown of tiny tentacles that acts as a filter for catching zooplankton. The fluffy anemone lives subtidally, where the slow tidal currents bend its crown over at right angles to the flow. In contrast, the great green anemone stands with most of its surface area parallel to the flow. At a given velocity both the size of the wake and the amount of drag are greater on a fluffy anemone than they are on a great green anemone with the same diameter of crown.

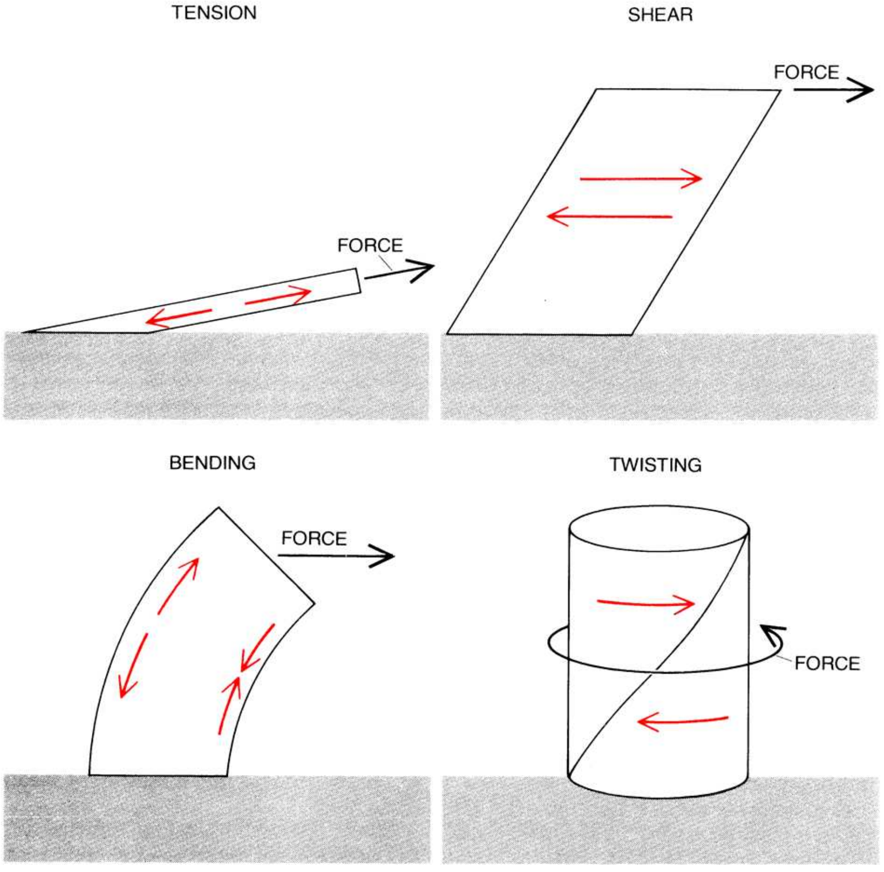
The branches and tentacles of many flexible marine animals and plants are pushed together as the organism is bent over by flowing water. The movement puts the organism more nearly parallel to the flow, reducing drag and the size of the wake. The fluffy anemone is an example: as the water flows faster the big tentacular crown collapses like an umbrella flipping inside out. A comparison of the drag on a fluffy-anemone model having a rigid crown with the drag on a model having a flexible crown reveals that the passive change of shape of the live anemone significantly reduces drag.

The drag forces on many large algae on wave-swept coasts are surprisingly low, notwithstanding the huge size of some of these seaweeds. Because of their flexibility the plants can be bent over parallel to the flow and are thus moved closer to the bottom, where the flow is slower. Flexibility also enables the seaweeds to employ another avoidance maneuver in waves. Since the plants move back and forth with the oscillating water, the water does not flow much with respect to them until they are completely flopped over in the direction of flow. The longer a seaweed is, the farther it is carried with the water before it is fully laid out in the direction of flow. If a seaweed is big enough, the water will start flowing in the opposite direction before the plant is fully bent over. Hence for large, flexible organisms in an oscillating flow an increase in length can lead to a decrease in drag.

Not all sessile organisms have drag-minimizing shapes. For example, certain gorgonian and alcyonacean corals form fan-shaped colonies that stand up at right angles to the direction of flow. These colonial animals feed on material suspended in the water passing them. The orientation of the colony in one plane perpendicular to the flow means not only that the colony is exposed to the maximum amount of flowing water per unit of time but also that it has no members downstream that would otherwise have to reprocess water depleted in food particles. Gordon Leversee, working at the Duke University Marine Laboratory, demonstrated that flat gorgonian corals captured more food when they were perpendicular to the flow than they did when they were parallel to it.

How do gorgonian sea fans achieve the correct orientation? Stephen A. Wainwright and John Dillon of Duke found that young sea fans are oriented every which way. They suggest that when moving water pushes on the growing fans, it tends to twist them until they are oriented perpendicular to the flow.

Sessile marine organisms in flowing water can also be subjected to lift forces. When the top surface of the organism curves upward, the water flowing over that surface must travel faster than the water flowing over other surfaces. The pressure in the fast-flowing region is lower than that in the other regions, and so the result is a force that tends to lift the organism off the substrate. Mark W. Denny of Stanford University has measured significant lift forces on various organisms, such as barnacles and limpets, that cling to rocks. By the same token, if the shape of an organism is such that the water flows faster around one side of it than around the other side, the organism is pulled toward the side where the flow is faster.



EFFECTS ON THE TISSUES of a sessile marine organism from the forces set up by the flow of water are tension (when the organism is pulled), shear, bending and twisting. The black arrows show the load on the organism; the colored arrows show the deformation of its tissues.

Still another force on many sessile organisms is the acceleration reaction. The water around a plant or an animal over which waves pass regularly speeds up, slows down and changes direction. The acceleration reaction pushes the organism in the direction in which the water is accelerating. (Bear in mind that when water slows down, it is accelerating in the direction opposite to its direction of movement.) The greater the volume of water that has to be accelerated to get around an organism, the stronger the acceleration reaction. A graph of the flow impinging on an organism in a wave shows that the maximum drag and the maximum acceleration reaction come at different times in the wave cycle. The force on an organism at any instant is the sum of the drag and the acceleration at that instant.

Examining the equations expressing the magnitude of the drag, lift and acceleration forces on sessile organisms, one can see that drag and lift are both proportional to the organism's area and that the acceleration reaction is proportional to the organism's volume. It would seem, then, that the acceleration reaction would become more important than drag or lift as an organism increases in size. Denny and Thomas Daniel of Duke and I suggest that acceleration-reaction forces may set an upper limit on the size many wave-swept organisms might achieve. Certainly many subtidal animals and plants, which live in slower and steadier currents than the intertidal organisms, do attain much larger sizes than the intertidal ones.

It may also be that wave action indirectly sets an upper limit on the size of certain organisms by restricting the amount of time the animals have to feed. Suzanne Miller of the University of Washington found that the force needed to dislodge various marine snails from a rock was smaller when they were moving over the surface than it was when they were still. If crashing waves cut short the time a snail has to move about and forage, the animal's growth may be limited. Similarly, the growth of an organism that feeds on particles suspended in the water may be limited if a violent flow makes it difficult for the organism to hold on to the food particles or makes the organism retract its delicate feeding structures.

Flow-induced forces sometimes deform or break an organism. Whether or not this happens depends on the magnitude of the stress (force per area) on the tissues of an organism in a flow and on the response of the tissues to the stress. The size and shape of an organism determine the magnitude of the stresses in its tissues when it bears a given load, such as a drag force. An attached plant or animal can bear the load in several ways, including tension, shear, bending and twisting.

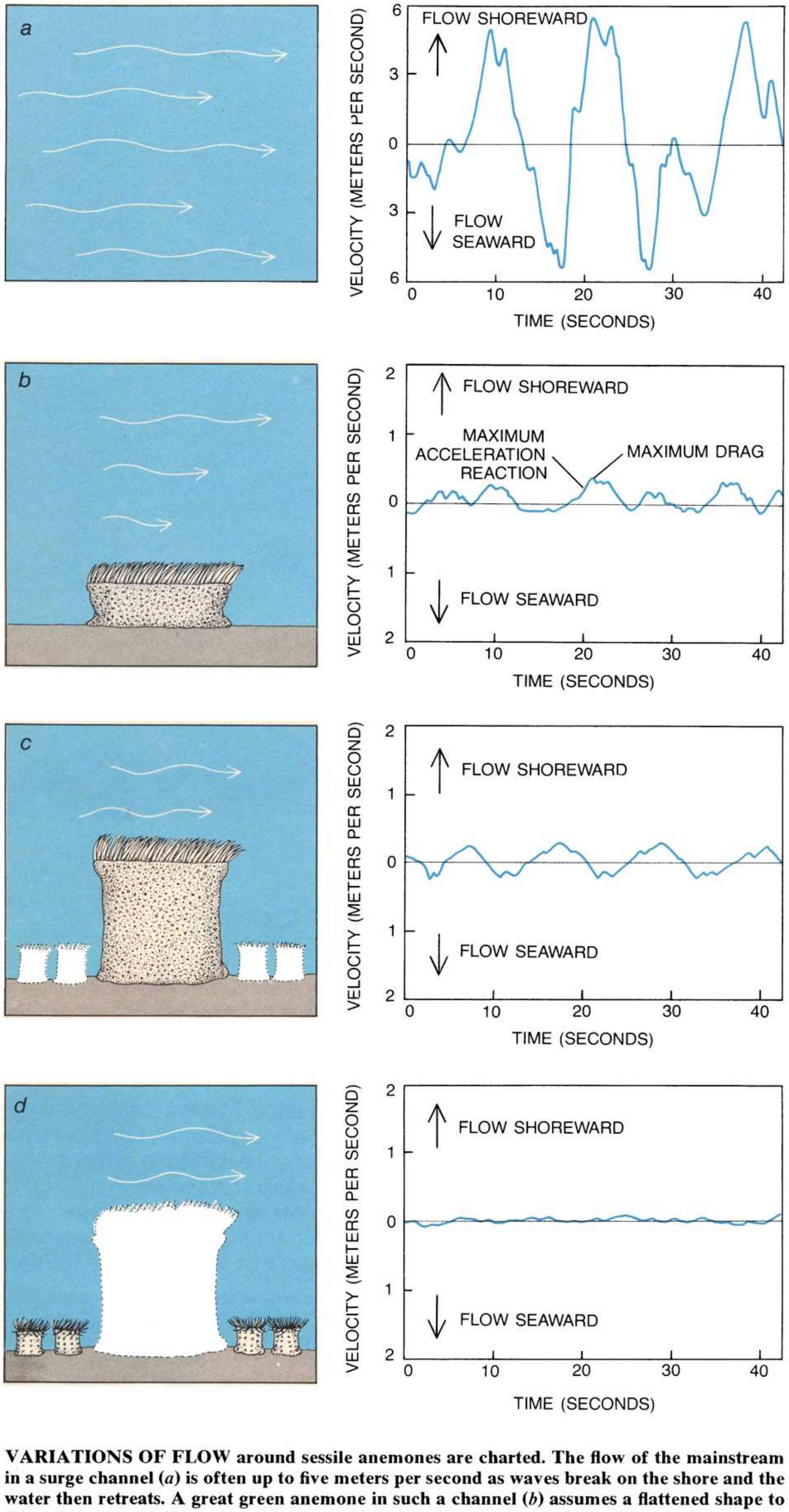
When an organism is sheared or pulled, the stresses in its tissues are inversely proportional to its cross-sectional area but are independent of its length and cross-sectional shape. The stresses in the tissues of a narrow organism are greater than those in a wider organism bearing the same load.

When an organism is bent by a load, one side of its body is stretched and the other is squashed. The tissues on the upstream and downstream surfaces are respectively the most pulled and the most compressed. The magnitude of the tensile or compressive stress at a point in the body of such a sessile organism is inversely proportional to the distance of that point from the free end of the organism. If two organisms of the same diameter but different height bear the same bending load, the stresses are greater in the taller one.

The magnitude of the tensile and compressive stresses associated with bending is inversely proportional to the cube of the radius of the organism. Hence a small increase in radius can significantly decrease the stress. It is not surprising that many organisms that stand upright in a moving fluid are widest and most heavily reinforced near their base. It is also not surprising that narrow constrictions in the stems of sessile organisms function as flexible joints.

A small increase in the radius of an organism twisted by a given torque also leads to a large increase in the torsional shear stresses. A thin organism therefore twists more readily than a thick one. Moreover, a narrow waist in the stalk of an organism can act as a rotational joint.

If you think about the large increase in stress in an organism that can accompany a small decrease in its radius, it becomes apparent the effect of a bite taken out of the stalk of a plant or an animal attached at a current-swept site can be potentially fatal. *Nereocystis leutkeana,* the giant bull kelp of the Pacific Northwest, provides a striking example of how disastrous the effect of such partial predation can be. Between 30 and 90 percent of the plants (depending on the location) that wash up on the shore have been broken at places in their stipes



VARIATIONS OF FLOW around sessile anemones are charted. The flow of the mainstream in a surge channel (*a*) is often up to five meters per second as waves break on the shore and the water then retreats. A great green anemone in such a channel (*b*) assumes a flattened shape to take advantage of the lower velocity of flow near the channel bottom. The maximum drag force on the anemone is exerted when the water velocity peaks, whereas the maximum acceleration-reaction force is exerted when the acceleration is greatest. (The acceleration is high when the slope of the tracing of velocity over time is steep.) In a protected site (*c*), where the brunt of the waves is borne by rocks to seaward, a great green anemone extends farther into the flow. The flow past it is much the same as the flow past the anemone in the surge channel. Even less flow is felt by some aggregating anemones (*d*) near the green anemone in the protected site.

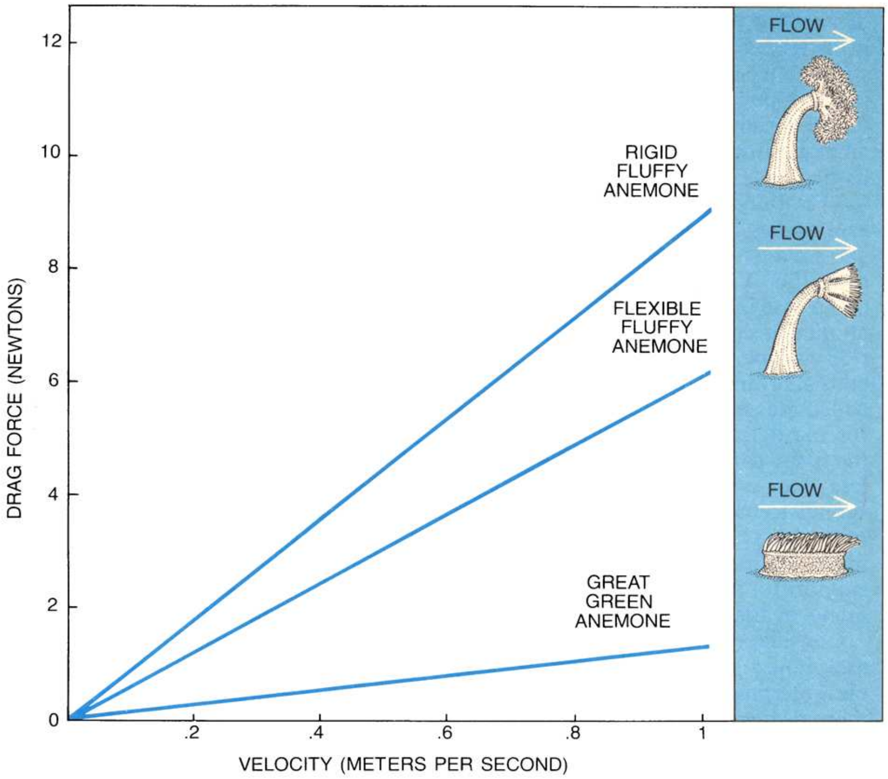
(stems) where only a small amount of tissue has been removed, usually by nibbling sea urchins.

The fluffy anemones and the great green anemones illustrate how profoundly the shape of an organism affects the stresses on it. The flow force on both the calm-water fluffy anemones and the surge-channel green anemones is about one newton (roughly a quarter of a pound) and tends to push the animals downstream. I have calculated, however, that under such a force the maximum stress in the tissues of a tall, slim fluffy anemone is 45 times greater than it is in an average short, wide green anemone. In other words, the fluffy anemone in the "protected" habitat is in a mechanically more stressful environment than the great green anemone in the "exposed" one.

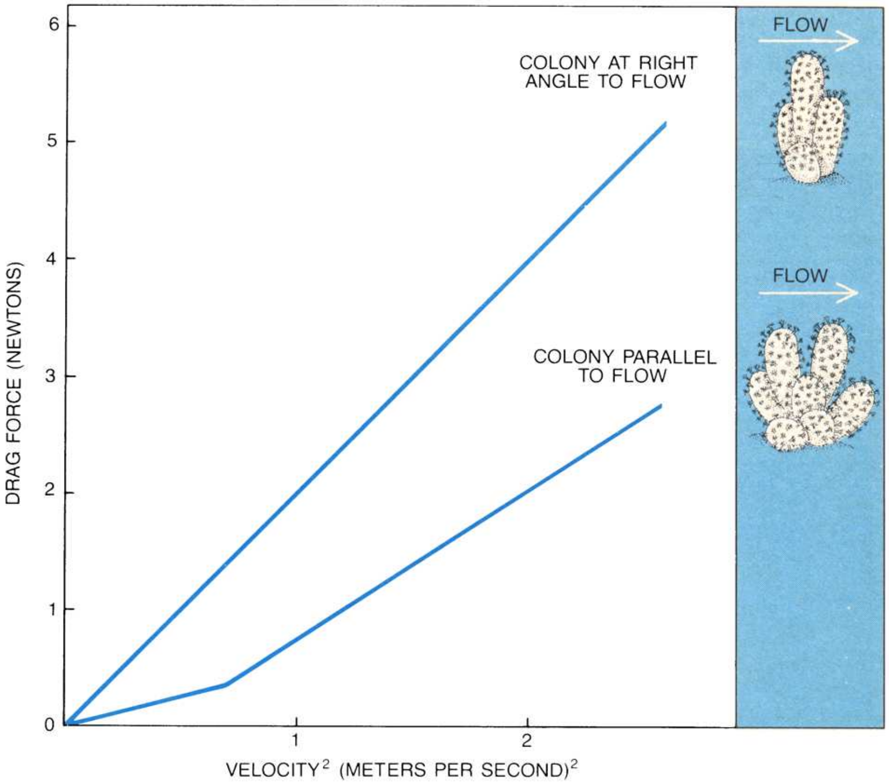
One can therefore see that a tall, narrow shape increases stress and a short, wide one decreases it. An organism can also reduce stress in its tissues by bearing loads in tension rather than by bending. An example is provided by two large seaweeds that form a dense band along the rocky shores of Chile. *Lessonia nigrescens* stands upright and is bent; *Durvillea antarctica* flops over at a narrow point near its holdfast and is pulled by moving water. I measured flow velocities of up to six meters per second across both species and forces of up to 20 newtons. A calculation of the maximum stress in a stipe 20 centimeters long and two centimeters in diameter, subjected to a load of 10 newtons, indicates that it is a third of a newton per square meter if the stipe is pulled (as *Durvillea* is) and more than 250 newtons if the stipe is bent (as *Lessonia* is).

The degree to which an organism deforms in flowing water depends not only on the magnitude of the stresses in its tissues but also on the stiffness of the tissues. Stiffness is measured by pulling a piece of tissue (in a device resembling a medieval torture rack) until it breaks. The apparatus measures both the force of the pull and the length to which the tissue has been stretched. A graph of the results shows that it takes more stress to pull a stiff tissue to a given extension than it does to pull a less stiff one. The slope of a stress-extension curve represents the elastic modulus of a material and provides a measure of the material's stiffness.

A peculiarity of many pliable biological materials is that their stiffness depends on the rate at which they are deformed (a dependence that does not hold with materials such as steel and glass). This characteristic is the basis of an interesting feature of the mechanical design of sessile organisms. As one might expect, a material deforms faster under a large stress than it does under a small one. The shape of an organism



WORK WITH MODELS shows that drag forces on anemones vary according to the configuration the animal presents to the flow of water. The drag on a model of a great green anemone, with most of its surface area parallel to the flow, is lower than the drag on the models of the fluffy anemone. The green anemone generates a smaller wake and so reduces form drag. The drag on a flexible model of the fluffy anemone, which, like the living animal, collapses into a more streamlined shape as the flow velocity increases, is lower than the drag on a rigid model.



DRAG FORCES on a colony of coral vary according to the orientation of the colony in the flow. The alcyonacean coral depicted here is *Alcyonium digitatum*, also known by the name dead-man's-fingers because it forms a fleshy colony that somewhat resembles a bloated hand.

determines the magnitude of the stress in its tissues, and the magnitude of the stress determines the rate of deformation, which in turn determines how stiff the material is. Therefore the shape of an organism can affect the stiffness of its tissues.

The fluffy sea anemone, *Metridium*, exemplifies how the stiffness of an organism's tissues is affected by the pace of its life. A tissue can be subjected to a creep test in which a constant stress is applied and the deformation over a period of time is measured. Sea anemones consist primarily of the gelatinous tissue called mesoglea. A graph of a creep test for mesoglea of *Metridium* shows that the tissue deforms little if it is pulled for less than a minute. The result corresponds to the time scale of the animal's muscular changes of shape. Hence the mesoglea provides a reasonably stiff support for the muscles and skeletal elements of the organism to work against.

Consider now a stress applied for several hours, the duration of the tidal currents pushing on the anemone. The mesoglea stretches increasingly and the anemone is bent passively in the direction of the flow. Over a period of between 12 and 24 hours the mesoglea can be stretched to three times its original length, even by small stresses. This long period corresponds to the time it takes for a fluffy anemone to inflate itself to the large sizes it can attain. (It does so by taking in water through grooves called siphonoglyphs, through which the water is pumped by beating cilia.) To a muscle working quickly the mesoglea is relatively stiff, but to a siphonoglyph working slowly it is quite compliant.

The creep curve for a piece of mesoglea from a great green anemone is notably different. Even if this anemone is beaten on by waves all day in a surge channel, it does not stretch much. The mesogleas of the two species of anemone show structural and molecular differences reflecting adaptations to the different mechanical conditions in their habitats.

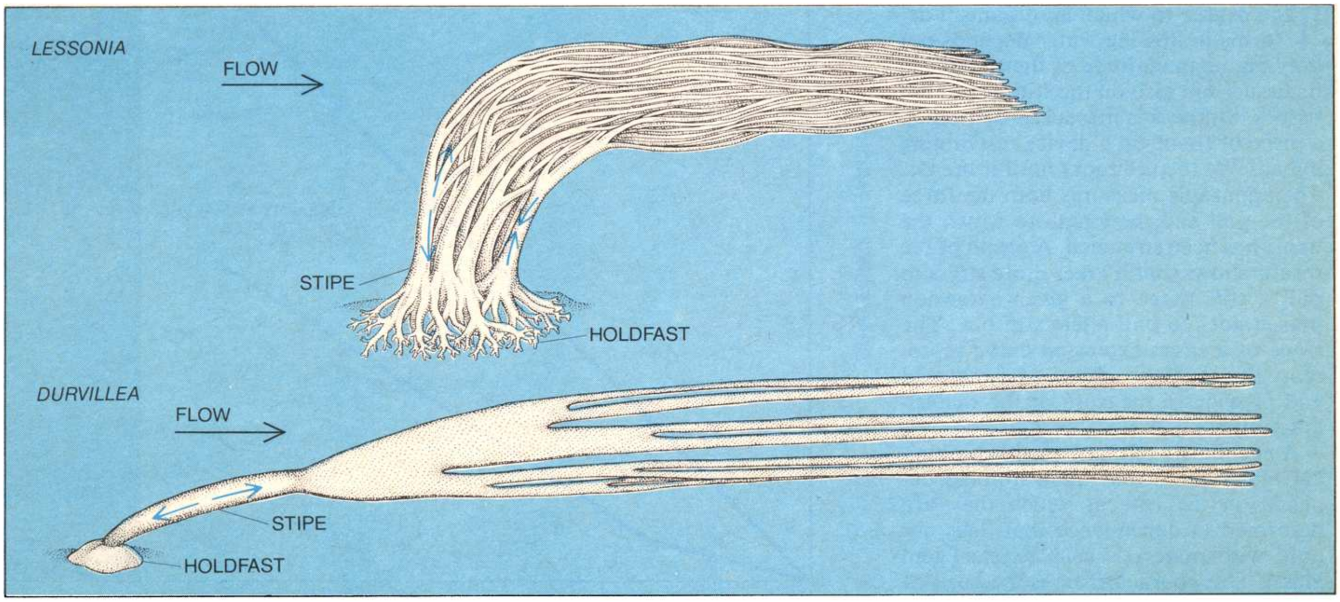
The supporting stalk of many attached plants and animals consists of more than one type of material. If the stiffest material is near the center of the stalk, the structure is more flexible than it would be if the material were at the periphery. Stephen Wainwright and I studied an example of a structure so flexible that it can easily be tied in knots without deforming. It is the stipe of the bull kelp, *Nereocystis*. The tissue near the center of the stipe is stiffer than the tissue at the periphery. This not only puts the main load-bearing tissue where it is less likely to be munched by sea urchins but also provides the flexibility that allows the kelp to be pushed over parallel to a fast current, reducing drag. In contrast, the stems of many terrestrial plants that stand upright (sunflowers, for example) have stiff vessels at their periphery.

The extent to which a sessile organism deforms in the water flow of a particular habitat has important effects on the success of the organism in its daily activities. Can it keep its tentacles in the appropriate configuration to catch food particles? Can it hold its photosynthesizing surfaces up above those of its competitors? Is it at risk of being injured or ripped from its substrate by the flow?

Whether or not a sessile organism will be broken away from its substrate depends not only on the magnitude of the stresses it encounters but also on the strength and toughness of its tissue and of the glue that holds it to the bottom. The strength of a material is defined as the stress required to break it. The likelihood that something will be broken by a wave or a current, however, depends on its toughness: the work required to break it. Glass may be stronger than leather, but a shoe is harder to break than a vase because leather is tougher than glass. The area under a stress-extension curve for a specimen that has been pulled until it breaks represents a measure of the work per volume of material necessary to achieve the break, that is, a measure of the toughness of the material.

A set of such curves reveals that there is more than one way to be tough. For example, the stiff, strong material from the stipe of the seaweed *Lessonia* is no tougher than the more compliant stipe of the seaweed *Durvillea*. These two algae illustrate two quite different strategies for resisting breakage. One is to be stiff and strong, as *Lessonia* is; the other is to be a "weakling" and to deform under stress, but to be able to extend a great deal before breaking, after the manner of *Durvillea*.

If a weakling is stressed for a long enough time to be stretched out to the breaking point, it will break at a lower stress than an organism that is stiff and tough. The weakling pattern of toughness is therefore more effective for organisms subjected to pulsing forces of



STRESS ON TISSUES of a sessile marine organism can be reduced if the organism bears loads in tension rather than by bending. Examples are provided by two large seaweeds that form a dense band along the rocky shores of Chile. *Lessonia nigrescens* is bent by moving water so that one side of its stipes is bent and the other is compressed; the maximum tensile and compressive stresses in a stipe are proportional to the length of the stipe and inversely proportional to the cube of its radius. *Durvillea antarctica* is pulled by moving water. The tensile stress in a stipe is independent of length and proportional to the square of the radius. The colored arrows represent the stresses.

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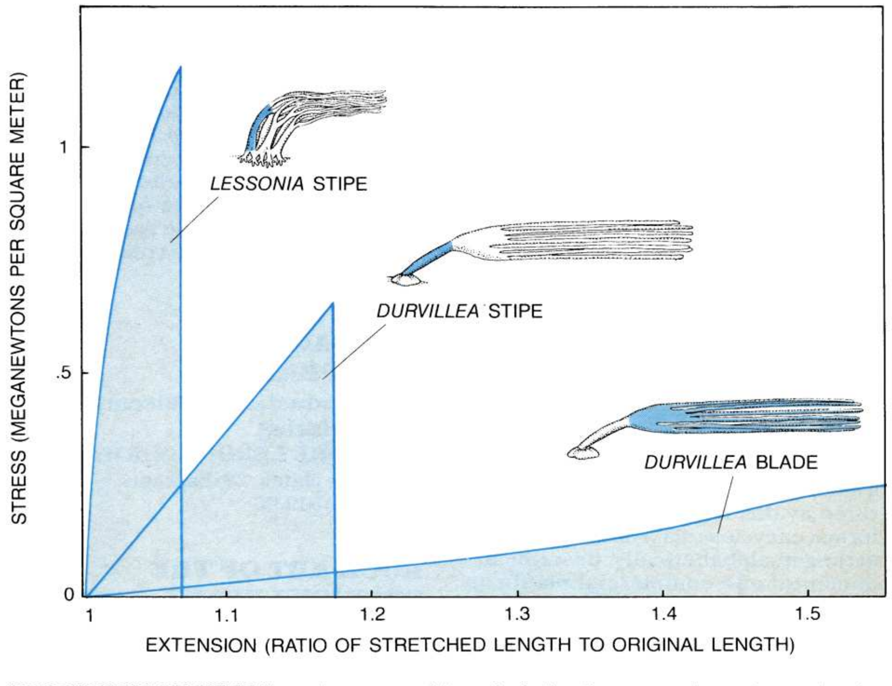
short duration, as on a shore beaten by waves. A weakling must also be resilient to survive: it must be able to recover to its resting shape before the next wave arrives. Many stretchy algae are highly resilient. For example, the stipe of the kelp *Nereocystis* can store as strain energy, and can employ for elastic recoil, about 75 percent of the energy that goes into stretching it. This stipe material is as resilient as elastin, the rubbery protein that enables human arteries to snap back into shape after each pulse of blood pumped by the heart.

I have designed mechanical tests to simulate the stresses sessile marine organisms encounter in nature. Compared with barnacles and stony corals, sea anemones are definitely in the weakling class; nevertheless, my simulation tests on mesoglea from the great green anemone of a surge channel indicate that this tissue is restored to its resting shape wave after wave. The mesoglea of the calm-water fluffy anemone does not recover as fast under the same stress, and after many cycles it can become so stretched out that it breaks. The fluffy anemone is a weakling-class organism that apparently lacks the resilience to survive in a surge channel.

A number of marine ecologists have described how physical disturbance is one of the important factors affecting the diversity of communities of sessile organisms. The patches of substrate cleared when organisms are broken away can be colonized by different plants and animals that might otherwise be excluded from the habitat by competitively more successful organisms. Those of us who studied the coral reefs of Jamaica before and after they were ravaged by Hurricane Allen in 1980 have a vivid picture of the role violent water motion can play in altering a community of organisms. As you might expect from my comments on the physical characteristics of sessile marine organisms, the tall, rigid corals of the reefs were smashed in the hurricane, whereas the lacy, flexible sea fans and the low-lying matlike algae survived (unless they were scraped away or buried by the rubble of the coral).

Books could be filled with examples of the weird and wonderful features of marine organisms that enable them to withstand and utilize moving water. The examples I have cited should illustrate that the marine biologist, armed with a few basic physical rules, can make considerable progress toward understanding the physical performance of organisms of different construction in different habitats. An exciting area that is just beginning to be explored is the role mechanical forces might play in the growth and development of organisms, perhaps helping to mold their bodies into the beautifully "engineered" adult forms seen in such abundance on shorelines and reefs.



TOUGHNESS OF TISSUE can be measured by calculating the area under a stress-extension curve of a tissue pulled until it breaks. The area represents the work per volume of material that is required to break the specimen. The calculations reveal there is no significant difference in the amount of work (74 kilojoules per cubic meter) required to break the tissues of the strong stipe of *Lessonia*, the more elastic stipe of *Durvillea* or the extensible blade of *Durvillea*. The measurements show that sessile marine organisms have more than one way of being tough.

ERRATA

Nereocystis luetkeana, pp. 61,62,67,68

Tunnicliffe, pp. 67,70

units for toughness of *L. nigrescens* & *D. antarctica*: $kJ \cdot m^{-3}$, p. 67

"fronds" should be replaced by "blades" on pp. 61,62,68