

18 Seaweeds in moving water: form and mechanical function

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Most macroalgae spend part of their lives attached to the substratum. The water moving around these sessile organisms carries dissolved gases and nutrients to them. Moving water can also remove waste products or sediments from the vicinity of a plant, and can disperse gametes or spores. Although seaweeds benefit from such external transport by ambient currents, they also risk being torn or dislodged by moving water. Hence, there are tradeoffs between living at sites exposed to rapid water flow and living at sites characterized by calm water.

Do morphological features that enhance an alga's ability to withstand moving water carry with them "costs" of reduced performance of other tasks, such as photosynthesis? The effects of specific structural features on defined aspects of an alga's performance must be quantitatively described before the costs and benefits of various morphologies can be evaluated for different environments. This chapter discusses ways in which certain mechanical aspects of an alga's performance in moving water depend on its structure. Specifically, I analyze how the morphology of a seaweed affects (1) the water flow it encounters, (2) the hydrodynamic forces it experiences, and (3) its deflection and breakage in flowing water. After the biomechanics of macroalgae are discussed, some examples of tradeoffs between decreasing the susceptibility of algae to mechanical damage and increasing their photosynthetic performance will be mentioned.

Water flow encountered by benthic algae

Flow habitats

There are several types of water-flow regimes that benthic algae encounter in different marine habitats (Bascom 1964; Carstens 1968; Riedl 1971; Neushul 1972; Wainwright and Koehl 1976). Perhaps the most obvious feature of water movement at many coastal sites is wave action (Figure 18.1). As a wave shape moves along the surface of the ocean,

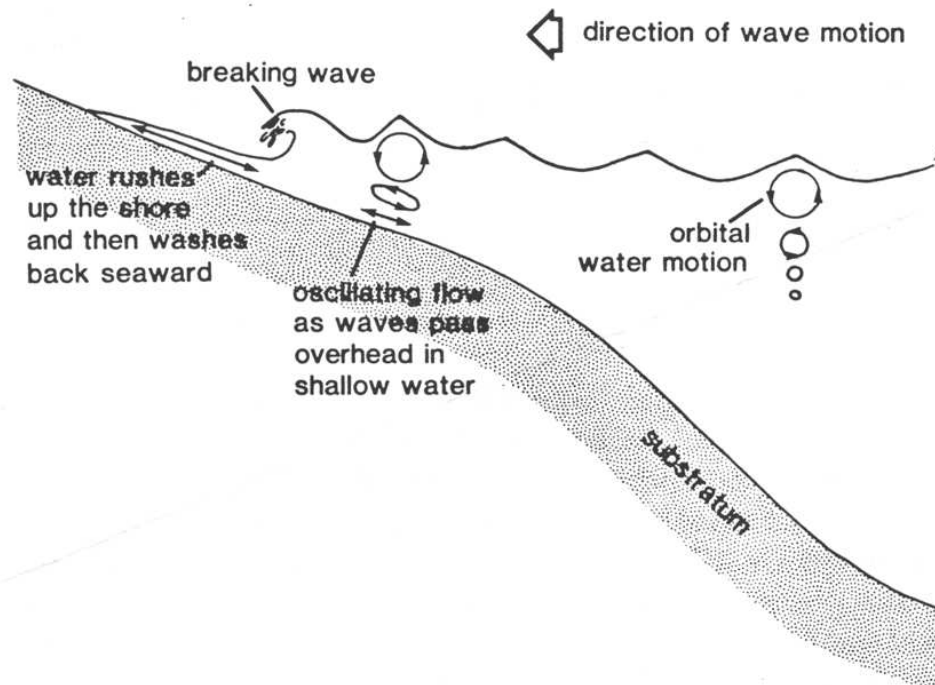


Figure 18.1. Diagram of the gross directions of water movement at a wave-swept shore, based on information presented by Bascom (1964), Carstens (1968), and Riedl (1971).

the water moves around locally in an orbital path. A giant kelp growing offshore with buoyant fronds near the water's surface encounters such orbital water movement. When waves move near a shore where the water depth is less than half the crest-to-crest distance of the waves, the orbital motion of the water is restricted near the substratum such that it oscillates back and forth as waves pass overhead. Shallow benthic algae encounter such bidirectional flows. Intertidal seaweeds are exposed to breaking waves and the consequent rapid surge of water up the shore, followed by seaward backwash. The water velocities and accelerations measured over organisms at low tide in breaking waves are greater than those they encounter when submerged at high tide with nonbreaking waves passing overhead (Koehl 1977a). If algae are growing in deep water or at sites protected from wave action, they may be in habitats subjected either to periodic tidal currents or to steady unidirectional currents.

Flow microhabitats

Within the various gross water-movement habitats described, the flow microhabitat of a particular alga depends on the form of the alga (Neushul 1972; Koehl 1984).

When water moves across the substratum, a velocity gradient exists between the bottom and the free-stream flow. Very small algae, such as newly settled spores or benthic diatoms, and very flat plants hugging the substratum, such as crustose coralline algae, may well be living in this boundary layer of slowly moving water (Neushul 1972; Wheeler and Neushul 1981; Norton et al. 1982). Immediately adjacent to the substratum, a viscous sublayer develops in which velocity is proportional to distance above the bottom. In most marine habitats, there is, above this sublayer, a turbulent boundary layer in which the average velocity increases with height above the substratum and in which flow is dominated by turbulent eddies. [For more detailed, quantitative descriptions of boundary-layer flow profiles, see Batchelor (1967) Schlichting (1968) Jumars and Nowell (1984), and Nowell and Jumars (1984).] The flow microhabitat encountered by an alga of a given height depends on a number of features of the site. For example, the faster or more unsteady the ambient flow and the rougher the substratum, the thinner the viscous sublayer. Furthermore, because a boundary layer builds up as water moves across a surface, the greater the distance between an alga and the leading edge of a structure (such as a rock or another alga) on which it sits, the thicker the boundary layer it encounters.

Even large algae can be in microhabitats that are protected from rapid ambient flow if they "hide" behind rocks or in crevices, or if they are surrounded by other organisms of similar size (Koehl 1976, 1977a, 1982). For example, water velocities within kelp beds (Wheeler 1980a, 1980b; Jackson and Winant 1983; M. Koehl, unpublished data) and seagrass beds (e.g., Peterson 1984) can be significantly lower than those outside the beds. Studies of air movement in plant canopies (e.g., Raupach and Thom 1981) and of water movement through arrays of coral branches (Chamberlain and Graus 1975), worm tubes (Eckman 1982; Jumars and Nowell 1984), and marsh grass (Eckman 1982, 1983; Fonseca et al. 1982) indicate that the size and spacing of neighbors can have profound effects on flow within a group of such structures. Furthermore, if organisms in an aggregation are flexible, they are bent over (and hence packed together more closely) in flowing water; such flexibility can reduce in-canopy flow velocities in seagrass meadows as water currents are redirected over, rather than through, the array of plants (Fonseca et al. 1982). Similar studies for arrays of structures of the sizes, shapes, flexibilities, and spacings of macroalgae remain to be done, although Anderson and Charters (1982) have described the effects on water flow of a single thallus of the bushy alga *Gelidium nudifrons*: Ambient turbulence is suppressed, but microturbu-

lence is generated in the alga's wake if the current is above a critical speed (which increases as the ratio of branch spacing to diameter increases).

Note that if algae are very short or are hidden among other structures, they not only avoid rapid water flow but also may be shaded from light by other organisms or topographic features. It should also be kept in mind that as an alga grows, it can encounter different water-flow microhabitats even though its position on the substratum is fixed (Neushul 1972; Wainwright and Koehl 1976; Norton et al. 1982).

Hydrodynamic forces on algae

Drag on algae in water currents

The shape and size of an alga affect not only the water flow it encounters but also the magnitudes of the forces it bears in that flow. The pattern of water flow around a body of a given shape, and hence the hydrodynamic force the body experiences, depends on the relative importance of inertia and viscosity, as given by the Reynolds number (Re) for that flow situation [$Re = (\rho UL)/\mu$, where ρ is the density and μ the viscosity of the water, U is the flow velocity, and L is a characteristic linear dimension of the body]. 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, tending to move it downstream. The drag on microscopic (i.e., low Re) and encrusting algae in moving water is due to skin friction. A low-pressure wake forms on the downstream side of macroscopic (i.e., high Re) upright algae in currents; hence, these plants are subjected to pressure drag (form drag) in addition to skin-friction drag (Hoerner 1965; Batchelor 1967; Vogel 1981). Any morphological feature of a macroscopic marine organism that reduces the size of the wake will reduce drag.

The magnitude of the total drag force (F_D) on a macroscopic organism is given by

$$F_D \propto C_D \rho U^2 S \quad (18.1)$$

where C_D is the drag coefficient of the organism (C_D depends in part on the shape of the plant), ρ is the density of the fluid, U is the velocity of water flow, and S is some characteristic area of the organism. Because drag is proportional to velocity squared, any of the features mentioned earlier that put an alga in a protected microhabitat can significantly reduce drag. Furthermore, an increase in size (S) is accompanied by an increase in drag for an alga in a unidirectional current. Algae of the same size, however, can

experience different drags in the same velocity of flow if they are of different shapes (C_D).

Most macroscopic algae are flexible and are deformed in moving water; such flexibility can reduce drag in several ways. For example, algal blades are bent over parallel to the direction of water movement and experience much less drag than would blades of the same area rigidly held normal to the flow. The C_D for a long, flat plate in the same range of Re values as macroalgae in tidal currents is more than 200 times greater when the plate is normal to the flow than when it is parallel (Vogel 1981). Furthermore, the blades on many algae can collapse on top of each other into a more compact shape as ambient velocities increase. Such passive streamlining has been shown to reduce drag in such diverse organisms as sea anemones (Koehl 1976, 1977a) and trees (Fraser 1962; Vogel 1984), as well as in algae (Charters et al. 1969; M. Koehl and R. Alberte, unpublished data). Even algae that do not fold up on top of themselves in a current can experience a reduction in drag if they are blown over close to the substratum, as illustrated by the red alga *Gigartina exasperata*. T. Mumford and I (unpublished data) found that the drag on *G. exasperata* near the substratum could be as low as half of that on the same plants encountering the same velocities, but not near the substratum (Figure 18.2). In both cases the algae flopped over parallel to the flow: Pressure drag was much reduced, but the plants still experienced skin friction. However, only the upper surfaces of the plants that were near the substratum were subjected to rapid flow and high skin friction, whereas both the upper and lower surfaces of plants held away from the substratum encountered rapid flow. In addition to drag reduction, another advantage of flexibility for algae in water currents is that thalli blown over prostrate on the substratum are less likely than are more upright, stiff thalli to be damaged by drifting objects, such as holdfasts of ripped-up algae (Dayton and Tegner 1984).

Mucilage secreted by seaweeds can reduce hydrodynamic forces in a number of ways. (1) Polymer coatings can reduce skin-friction drag (e.g., Wells 1969; Cox et al. 1974), as mucus does on fish (e.g., Daniel 1981). Although Norton et al. (1981, 1982) have suggested that mucilage on algal surfaces may reduce skin friction, my comparisons of drag measured on mucilage-covered kelp (Koehl, unpublished data) and on mucus-covered sea anemones (Koehl 1977a) with drag on nonslimy models of the organisms indicate that such coatings have a negligible effect on the total drag. However, other species must be studied at a range of Reynolds numbers before the importance of mucilage coatings in reducing drag on macroalgae can be evaluated. (2) The hydrodynamic forces on seaweeds can be increased when they bear epiphytes (e.g., Sousa 1979). Therefore, if a

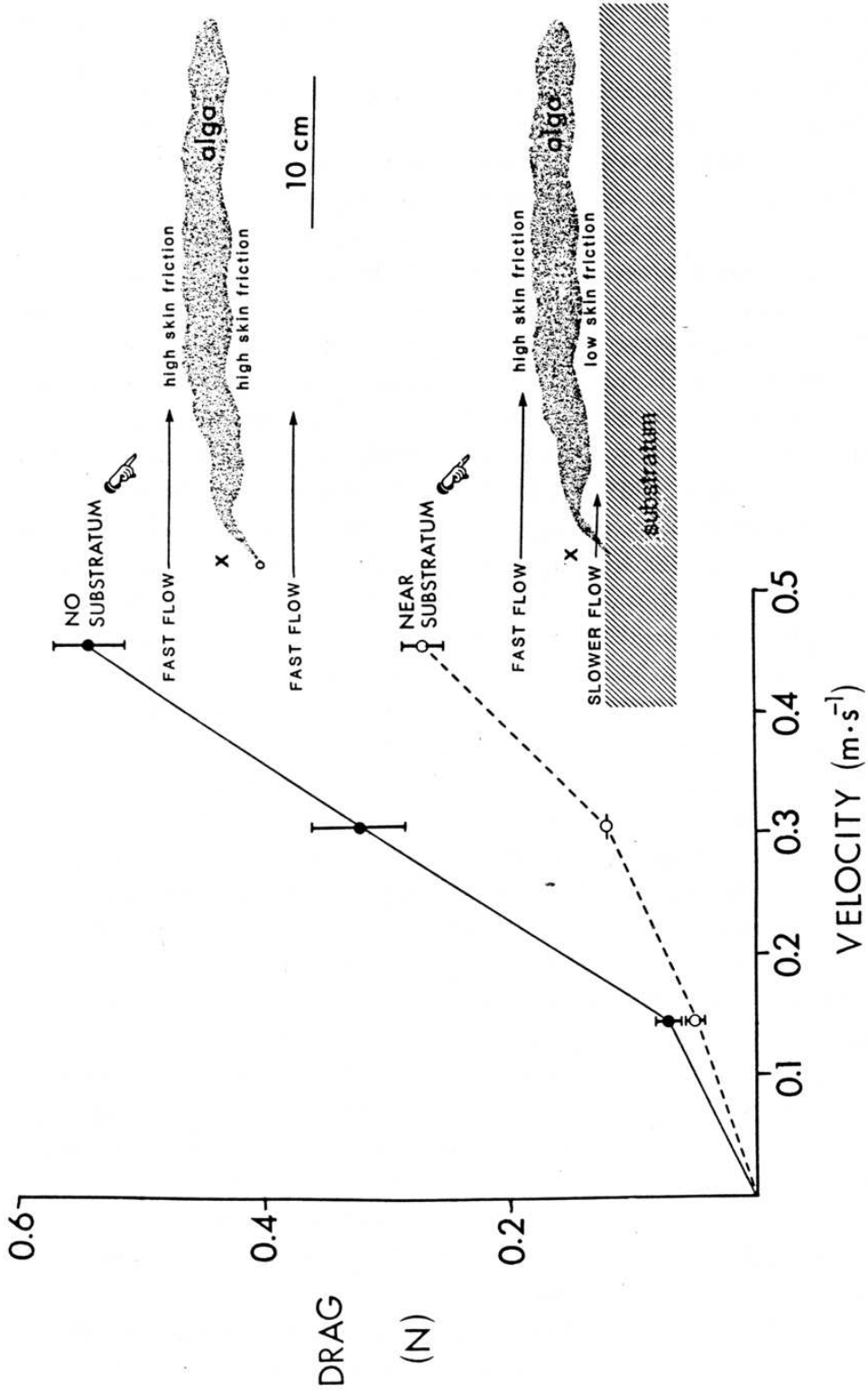


Figure 18.2. Drag forces measured on a *Gigartina exasperata* when next to and not next to a substratum. Water velocities were measured just upstream from the alga at the height of the blade when it was blown over (position indicated by X). Error bars indicate one standard deviation (graph redrawn from Koehl 1984).

mucilaginous secretion reduces the attachment of epiphytes on an alga's surface, the secretion can indirectly reduce the drag the host plant has to bear. (3) Films of organic surfactants on the water surface can suppress wave motions (e.g., Van Dorn 1953; Vines 1960). Deacon (1979) has suggested that mucus secreted by corals can form a surface film that will reduce wave damage to reefs by this mechanism. Perhaps the surface slicks that sometimes form over kelp beds (Sturdy and Fischer 1966) can reduce the wave-associated water flow encountered by the kelp.

Forces on algae in waves

Intertidal and high subtidal seaweeds exposed to wave action experience accelerating water. Wave-swept organisms are subjected to acceleration reaction forces as well as to drag (Keulegan and Carpenter 1958; Wiegel 1964; Batchelor 1967; Carstens 1968). The pressure differential on a body in a fluid subjected to gravity gives rise to a buoyant force on that 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 an animal accelerates through a fluid, its motion affects some volume of fluid such that the animal exerts force to accelerate not only its own mass but also an "added mass" of fluid. Similarly, when water accelerates with respect to a stationary plant, this added mass contributes to the force the plant experiences.

The acceleration reaction force (F_I), which is a combination of the virtual buoyancy and the force due to added mass, is given by

$$F_I \propto C_M \rho V dU/dt \quad (18.2)$$

where C_M is the added-mass coefficient of the body (dependent in part on shape), ρ is the density of the water, V is the volume of the organism, and dU/dt is the acceleration of the water. The acceleration reaction acts in the direction the water is accelerating, that is, in the direction of water movement when it is speeding up, but in the opposite direction when it is slowing down. The force on a wave-swept organism at any instant in time is the sum of the drag force at that instant and the acceleration reaction at that instant.

Because the acceleration reaction is proportional to the volume of an organism, we might expect it to become increasingly important with respect to drag (which is proportional to area) as organisms get larger, and to impose a physical upper limit to the sizes wave-swept organisms can attain (Denny et al. 1985). Macroalgae, which are often the largest organisms on

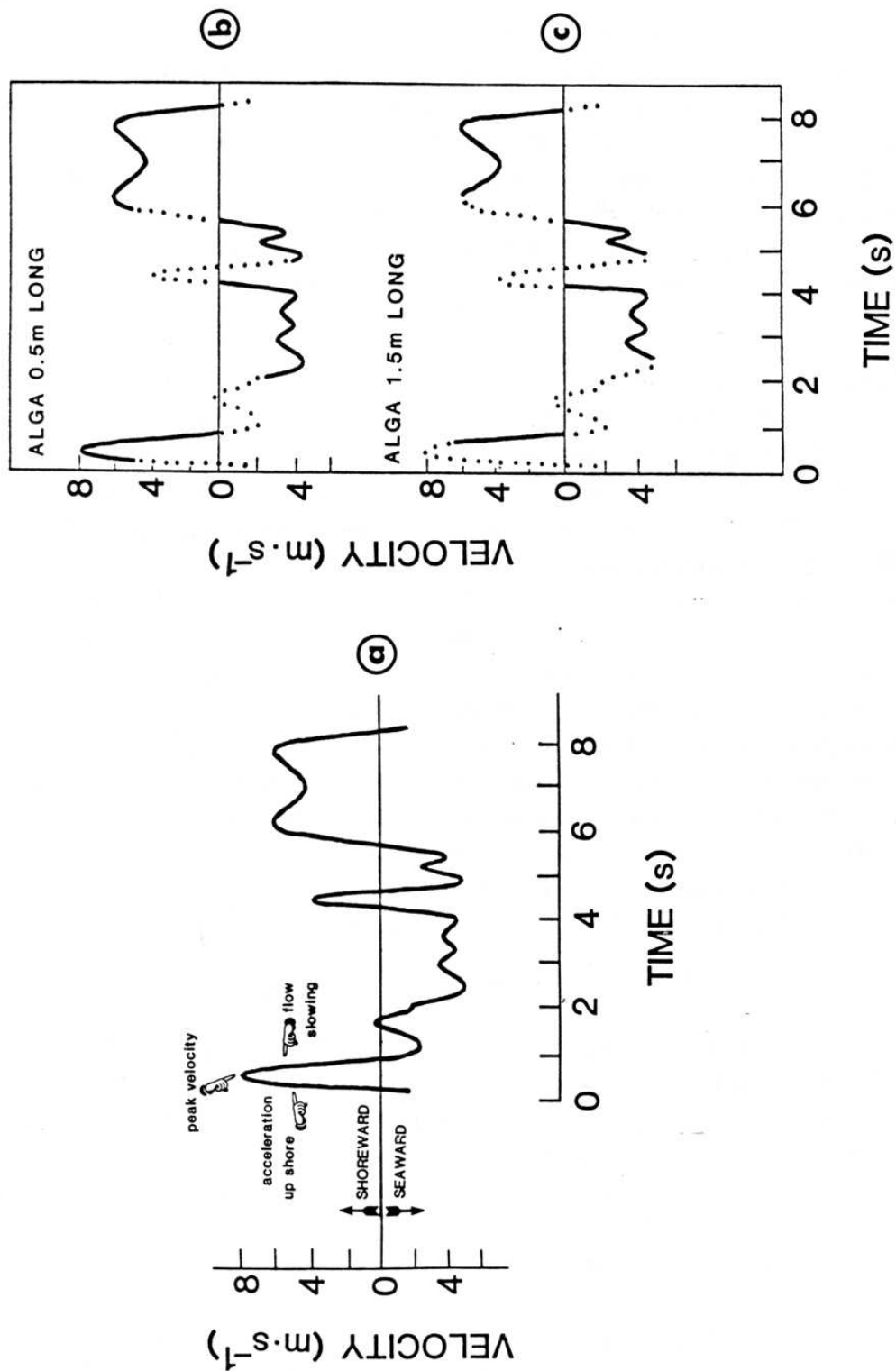


Figure 18.3. Water velocity versus time measured 15 cm above the substratum at a rocky shore on Tatoosh Island, Washington, where *Postelsia palmaeformis* and *Lessoniopsis littoralis* were abundant. (a) Water movement relative to a rigid structure. (b) Dotted lines indicate water movement at times when a perfectly flexible alga 0.5 m long would be moving with the water. Solid lines indicate water movement relative to the thallus at times after the plant would be fully laid out in the direction of flow. The thallus must resist forces produced by the water movement indicated by solid lines. (c) Notation as in (b), but for a plant 1.5 m long.

temperate wave-beaten rocky shores, have several morphological features that tend to reduce the acceleration reaction. For example, the blades of most macroalgae are thin; hence, their volumes are low even though they can be quite large in area. Furthermore, the C_M for flattened bodies oriented parallel to the acceleration is lower than the C_M for spherical bodies or for flattened objects normal to the acceleration (Daniel 1983, 1984). Most macroalgae not only have relatively flat blades but also are flexible and become passively oriented parallel to flow, as described earlier.

The flexibility of large algae at wave-swept sites also provides a mechanism by which the thalli can avoid bearing flow-induced forces at times during a wave when they are likely to be highest. An example of water velocities recorded among seaweed blades at a wave-swept rocky intertidal site is shown in Figure 18.3a; the maximum drag should occur when such a plot of velocity versus time peaks ($F_D \propto U^2$), whereas the maximum acceleration reaction should occur when the slope is steepest ($F_I \propto dU/dt$). However, as the water in a wave accelerates, the forces it imposes on a floppy alga move the plant along with the water; not until the attached plant is strung out in the direction of flow and is no longer free to move with the water does its thallus have to resist substantial force. If a flexible alga is long enough, the water may slow down or move back in the opposite direction before the slack in the plant has been taken up. Figure 18.3b,c illustrates that an increase in the length of a flexible seaweed can lead to a decrease in the forces its thallus must resist in oscillating flow. [In contrast, an increase in the length of an alga in unidirectional flow leads to an increase in the load (drag force) the thallus must bear.] Furthermore, even if a flexible plant is not long enough to totally avoid the peak accelerations and velocities of water in waves, the duration of flow relative to the plant (and hence the duration of high loads on the thallus) is less than if the alga were rigid (the consequences of this for plant breakage will be described later). Of course, the stiffer a seaweed of a given length, the sooner there will be water movement relative to its surfaces as a wave rushes in to shore.

Deflection and breakage

Just as water-flow patterns around and flow-induced forces on macroalgae depend on their morphology, so do their deformation and possible breakage. Engineering analyses can be used to elucidate aspects of algal structure that affect the deflection or breakability of the plants. Nonetheless, how these two aspects of mechanical performance relate to

the success of various seaweeds in different habitats can be assessed only if the physiology, reproductive biology, and ecological interactions of the algae are also known. Is a stiff plant able to hold its blades above those of its more flexible neighbors, thereby out-competing them for light? Is a flexible plant flailing back and forth in waves able to lash off epiphytes (Fletcher and Day 1983) or fling off herbivores, such as snails or sea urchins, more readily than stiffer algae? Is a flexible seaweed more effective than a stiff one at sweeping the surrounding substratum clear of newly settled potential competitors (e.g., Dayton 1975; Velimirov and Griffiths 1979)? Does breakage mean death for a plant, or can the stump regrow? Can the broken-off fragments, or the spores they carry, attach to the substratum and grow [i.e., is fracture a mechanism of asexual reproduction and dispersal for seaweeds (e.g., Norton et al. 1982) as it is for many corals (e.g., Highsmith 1982)]? Has an alga released its spores or gametes before seasonally predictable periods of high mechanical stress occur?

In analyzing both deflection and breakage of seaweeds, one needs to consider how the shape of an alga affects the magnitude and distribution of mechanical stresses in its thallus and how the material properties (e.g., stiffness, strength, toughness, resilience) of its tissues determine an alga's response to those stresses. Mechanical stress is defined as the force per cross-sectional area of tissue bearing that force.

Stress in an algal thallus

Sessile organisms in moving water can be deformed in a number of ways, as illustrated in Figure 18.4. The stresses in the organism for a given load, such as drag force, depend on the shape and size of the organism (Koehl 1977b, 1982, 1984). Some basic relationships between stress and certain morphological parameters will be presented later. For simplicity of discussion, we shall assume that the force is applied to an alga at a point and that the alga undergoes small deformation. [Of course, real algae can bear distributed loads and can deform a great deal. Specific equations describing stress distributions in structures of various shapes under different loading regimes can be found in engineering books (e.g., Popov 1968; Timoshenko and Gere 1972; Roark and Young 1975; Faupel and Fisher 1981), and an example of stress analysis of an algal stipe undergoing large deformations can be found in the work of Charters et al. (1969).]

If an alga is simply pulled by water currents (Figure 18.4), the magnitude of the tensile stress (σ) in its tissues is

$$\sigma \propto 1/A \quad (18.3)$$

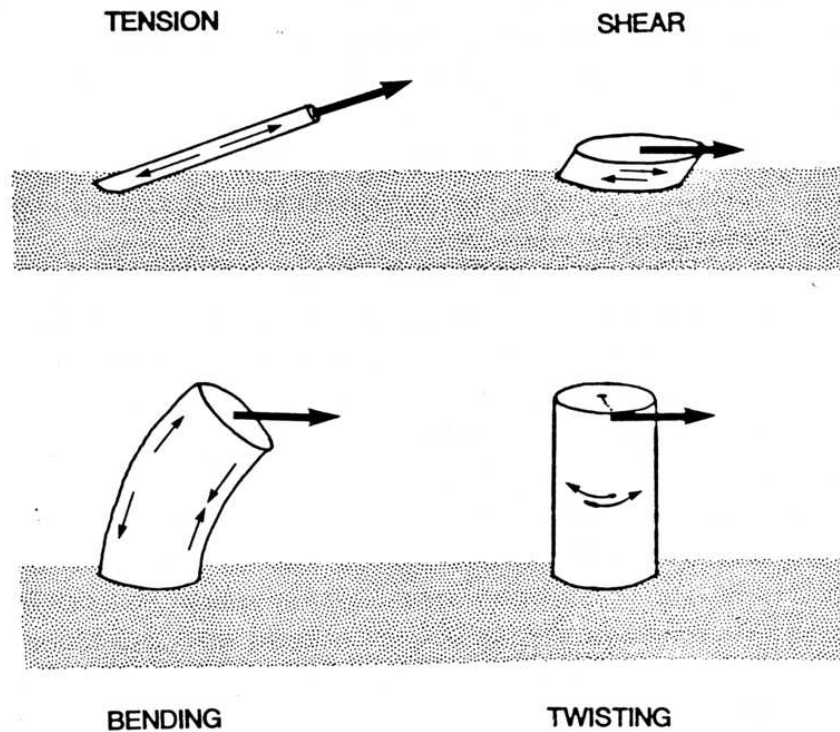


Figure 18.4. Diagrams of some of the ways a sessile organism can deform when bearing a load such as a hydrodynamic force. Heavy arrows indicate the direction of force application, and fine arrows indicate the deformation of the organism's tissues.

where A is the cross-sectional area of the plant. Similarly, if an alga is deformed in shear (Figure 18.4), the magnitude of the shear stress (τ) in its tissues is

$$\tau \propto 1/A \quad (18.4)$$

In both cases, the greater the cross-sectional area of the plant, the lower the stress, but cross-sectional shape is relatively unimportant. Tissues in narrow regions of a plant will be subjected to greater stresses than tissues in wide regions of the thallus.

If an alga is bent in a current (Figure 18.4), the tissue on its upstream side is stretched, and that on its downstream side is compressed. The tensile or compressive stress (σ) in the plant is

$$\sigma \propto hy/I \quad (18.5)$$

where h is the distance of the bit of tissue being considered from the free end of the sessile organism, y is the distance from the axis of bending, and I is the second moment of area of the cross-section of the organism (Alex-

ander 1968; Wainwright et al. 1976). Because stress is proportional to h , the stresses in tissues near the attached end of an alga bent by flowing water are greater than those near its free end (if it has the same cross-sectional shape and area, base to tip). Similarly, if two stipes of the same cross-sectional shape and area are bent by loads of the same magnitude, but one stipe is taller than the other, the maximum stress in the tall stipe will be greater than that in the short one.

Tissues on the upstream and downstream surfaces of a bent alga are stretched or compressed more than tissues closer to the axis of bending of the plant ($\sigma \propto y$). Because such peripheral tissue contributes more to bearing the load than does tissue near the axis of bending, the more tissue a plant has far from the axis of bending, the lower the stress that any little bit of tissue within the plant has to bear. The second moment of area (I) is a measure of the distribution of tissue around the axis of bending of an organism and is roughly proportional to the radius raised to the fourth power. Therefore, the cross-sectional shape of a bent alga can have a big effect on the stresses in its tissues. For example, if an alga invests a given area of tissue in a cross section of its stipe, the stress for a given load will be lower if the stipe is elliptical in cross-sectional shape with its major axis parallel to the direction of ambient currents than if the stipe is circular in cross section. Similarly, for an alga in a habitat in which flow direction is not predictable, for a given cross-sectional area the stress produced by a particular load will be lower if the stipe is hollow and wide than if it is solid and narrow (Currey 1970). Furthermore, because stress in a bit of tissue is roughly inversely proportional to the radius raised to the third power ($\sigma \propto y/I$), a small increase in the width of an organism can lead to a large decrease in the stress in its tissues for a given load. Similarly, a narrow "waistline" in an algal thallus can be a region of much higher stress than wider parts of the thallus.

If an alga is twisted by moving water (Figure 18.4), the shear stress (τ) in a bit of its tissue is

$$\tau \propto My/J \quad (18.6)$$

where M is the distance (moment arm) of force application from the axis of torsion, and J is the polar second moment of area of the cross section of the plant. J , like I , is roughly proportional to the radius raised to the fourth power (Wainwright et al. 1976). As in the case of bending, tissues around the periphery of a twisted alga bear the largest stresses ($\tau \propto y$), and a small decrease in thallus width can lead to a large increase in stress. Furthermore, asymmetrical plants and plants with wide, stiff blades on narrow

stipes are likely to experience higher torsional shear stresses than are plants with lower M values.

Although stresses in hollow, wide organisms are lower than those in solid, narrow ones under a given load in bending or twisting, hollow, thin-walled structures tend to undergo local buckling (i.e., kink like a beer can) (Currey 1970; Wainwright et al. 1976; Koehl 1977b). The critical stress (σ_{crit}) to produce local buckling in a bending hollow cylinder is

$$\sigma_{\text{crit}} \propto t/d \quad (18.7)$$

where d is the diameter and t is the wall thickness (i.e., wide, thin-walled cylinders kink at lower stresses than do narrow, thick-walled ones). Hence, the "benefit" of stress reduction for a given investment in material obtained by an increase in d (and hence a reduction in t) is offset at some point by the risk of local buckling; see Currey (1970) for a discussion.

Keeping in mind these simple relationships between the magnitude of stress in an alga's tissues and its size and shape, consider some examples:

Algae often break at regions where grazers have taken bites out of them (e.g., Black 1976; Koehl and Wainwright 1977; Koehl 1979; Santelices et al. 1980). Because removal of a small amount of peripheral tissue can lead to large decreases in I and J , it should not be surprising that stresses in regions of a thallus where bites have been taken can reach the breaking point under bending or twisting loads that would not damage the intact plant. Because of this simple mechanical fact of life, the loss of algal biomass from a stretch of shore because of the activities of herbivores can be much greater than the plant tissue they consume. Nonetheless, "pruning" by grazers can in certain cases decrease the likelihood that an entire plant will be ripped off the substratum during a storm, because as pieces of an alga are broken off, the flow force on the remaining smaller thallus can be reduced (Black 1976; Santelices et al. 1980).

Stresses associated with bending depend on length and cross-sectional shape, whereas those associated with pulling do not. Therefore, if the long, slim stipe of an alga bears a load in tension, the stresses in its tissues can be lower than if it bears that same load in bending. An example of this point is provided by two species of macroalgae abundant on the wave-swept rocky shores of central and southern Chile, *Lessonia nigrescens* and *Durvillaea antarctica*. These seaweeds experience similar ranges of flow forces in situ (Koehl 1979, 1982, unpublished data). Santelices et al. (1980) have pointed out that a *Lessonia* bears its blades (and hence the hydrodynamic force on the blades) on several stipes, whereas a *Durvillaea* bears the whole force on only one stipe; they suggest, therefore, that *Lessonia* has a mor-

phology better suited to withstanding wave action. However, *Lessonia* stipes, which are widest near their bases and are relatively stiff, are bent by flowing water, whereas *Durvillaea* stipes flop over at a flexible joint at the holdfast and are pulled by ambient currents. Calculation of the maximum stresses in stipes of a *Lessonia* and a *Durvillaea* of the same length and mean diameter indicates that stresses in the bent stipe are over 800 times greater than those in the pulled one when they bear the same load (Koehl 1982). It appears, therefore, that both species have stress-reducing thallus shapes.

Deformation of an alga in moving water

The amount of deformation an alga undergoes when bearing a flow-induced force depends not only on the shape of the thallus but also on the stiffness of its tissues. For example, the lateral deflection (δ) of the free end of a sessile organism bent by a force is

$$\delta \propto h^3/EI \quad (18.8)$$

where h is the height of the organism, and E is the tensile elastic modulus of the tissues, a measure of their stiffness. Similarly, the angular deflection (θ) of the free end of an alga twisted by a load (F) is

$$\theta \propto Mh/GJ \quad (18.9)$$

where G is the shear elastic modulus. Algae with tall, slim thalli (high h , low I and J) have deflection-increasing morphologies, whereas algae with short, wide thalli (low h , high I and J) have deflection-decreasing body shapes.

An alga can decrease the amount it deforms for a given load by changing its shape (i.e., decreasing h/I and h/J) and/or by increasing the stiffness of its tissues (E and G). Several species of macroalgae have been observed to produce shorter, wider stipes at sites exposed to rapid water flow than they produce at more protected sites (e.g., Mann 1971; Chapman 1973; Gerard and Mann 1979). Similarly, the tissues of exposed algae of some species have been found to have higher elastic moduli than the tissues of protected members of the same species (e.g., Charters et al. 1969; Armstrong 1982).

If localized portions of a thallus are made of easily deformable tissue (i.e., of low E or G) and/or if certain sections of an alga are narrower (i.e., have lower I and J) than the rest of the thallus, these regions can behave as flexible joints (Koehl 1977b). Examples of the former are the deformable genicula between the heavily calcified rigid sections of upright coralline algae such as *Calliarthron tuberculosum* (R. B. Emler, unpublished data). Examples of the latter are the joints between the stipes and holdfasts of *Durvillaea antarctica* (Koehl 1982; Norton et al. 1982). Therefore, the

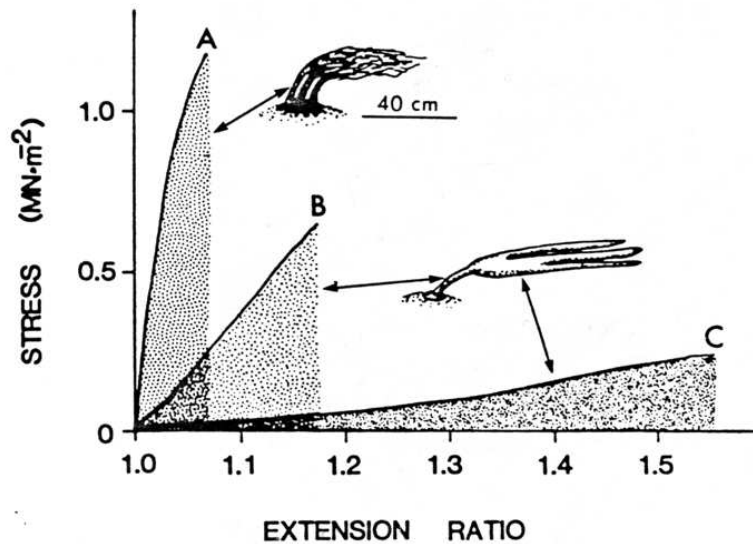


Figure 18.5. Stress–extension-ratio curves for tissues from *Lessonia nigrescens* stipe (A) and *Durvillaea antarctica* stipe (B) and blade (C) (redrawn from Koehl 1982). Both seaweeds are drawn to the same scale. Extension ratio is the ratio of the extended length of a specimen to its unstretched length.

structure of an alga can determine the location on a thallus at which deformation will occur, as well as the amount of deflection produced by a given load.

The stiffness of algal tissue can be measured by pulling on a sample of the tissue at a defined rate and simultaneously measuring the force with which the tissue resists the pull (Koehl and Wainwright in press). Results of such measurements for tissues from the Chilean seaweeds *Lessonia nigrescens* and *Durvillaea antarctica* are presented in Figure 18.5. The more resistant a tissue is to deformation, the steeper will be the slope of such a stress–extension-ratio curve; E , which is the slope of a stress–extension-ratio curve, is a measure of tissue stiffness. (Similar tests can be done in shear to measure G .) The stipe tissue of *Lessonia* is stiffer than that of *Durvillaea*, which in turn is stiffer than its blade tissue.

The stiffness of a tissue depends on its microscopic structure and molecular structure. Much remains to be learned about the ways in which algae build stiff or stretchy tissues out of fiber-reinforced cell walls and intercellular matrix. The ultrastructure, chemical composition, and mechanical properties of algal cell walls are beyond the scope of this chapter, but reviews of these topics can be found in the work of Preston (1974), Wainwright et al. (1976), Sellen (1980), McCandless (1981), and Vincent (1982). I shall briefly point out, however, some patterns I have noticed in the microscopic structures of stiff versus stretchy seaweed tissues I have

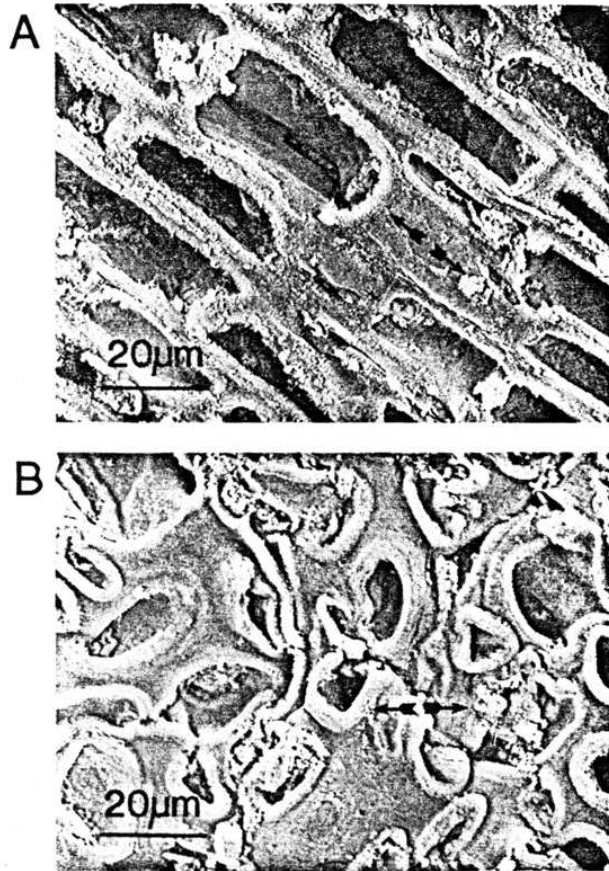


Figure 18.6. Scanning electron micrographs of transverse sections of stipe tissue from (A) *Lessonia nigrescens* and (B) *Durvillaea antarctica*. Arrows indicate radial direction.

studied. Stiff tissues, such as from the stipes of *Lessonia*, have closely packed cells with thick cell walls that appear to be continuous from cell to cell parallel to the major stress axes in the tissue (Figure 18.6A). In contrast, stretchy tissues, such as from the stipes of *Durvillaea*, tend to have thin-walled cells with large areas of intercellular matrix between them (Figure 18.6B). The tremendous extensions that such stretchy algal tissues can undergo may occur by movement of cells relative to each other as the intercellular matrix is sheared. The incredibly stretchable blades of *Durvillaea* are composed of a honeycomb of air sacs that are easily deformed from roughly spherical to roughly ellipsoidal in shape as the tissue is stretched.

The chemistry of the intercellular matrix can affect its resistance to deformation. For example, the polysaccharide alginate is the major intercellular substance in most brown algae. L-guluronic acid residues in algin-

Table 18.1. Strength and toughness of seaweed tissues and other biomaterials^a

Material	Strength (MN/m ²)	Toughness (kJ/m ²)
Seaweed tissues		
<i>Durvillaea antarctica</i>	0.7 ₁	4 ₁
<i>Laminaria digitata</i>	0.9 ₂	— ^b
<i>Lessonia nigrescens</i>	1.2 ₁	4 ₁
<i>Ascophyllum nodosum</i>	1.5 ₂	—
<i>Nereocystis luetkeana</i>	3.6 ₃	—
<i>Fucus serratus</i>	4.2 ₂	—
Other biomaterials		
Mammalian skin	12 (cat) ₄	20 (rabbit) _{5,t}
Whale tympanic bulla	33 _{5,b}	0.2 _{5,b}
Insect cuticle	95 (<i>Schistocerca tibia</i>) ₄	1.4 (<i>Rhodnius tergum</i>) _{5,t}
Deer antler	179 _{5,b}	6.2 _{5,b}
Softwood	180 ₅	12 ₅
Tooth enamel	200 _{5,c}	0.2 _{5,b}
Cow leg bone	247 _{5,b} , 184 ₄	1.7 _{5,b}
Hardwood	240 ₅	11 ₅
Tooth dentine	300 _{5,c}	0.6 _{5,b}

^a All materials were tested in tension except where indicated by one of the following subscripts: b = bending, c = compression, and t = tearing. Results from specimens tested in different ways are not strictly comparable. Numerical subscripts indicate the source of the values reported: 1 = Koehl (1979); 2 = Wheeler and Neushul (1981); 3 = Koehl and Wainwright (1977); 4 = Wainwright et al. (1976); 5 = Vincent (1982).

^b Data not available.

ate are responsible for the formation of junctions in alginate gels produced in the lab; within- and between-species comparisons indicate that brown algal tissues are stiffer when their alginates are rich in L-guluronic acid residues than when their alginates contain small proportions of these residues (Haug, Larsen, and Baardseth 1969; Andreson et al. 1977).

The stiffnesses of many biological materials and the permanence of deformations imposed on them can depend on the rate at which they are deformed as well as on their history of load bearing. Little information is available on the possible viscoelastic, stress-softening, or plastic behaviors of seaweed tissues of different microarchitectures.

Breakage of an alga in moving water

The strength of a tissue is defined as the stress required to break it. Compared with other biomaterials, the tensile strengths of seaweeds are low (Table 18.1) (Delf 1932; Koehl and Wainwright 1977; Norton et al. 1981; Wheeler and Neushul 1981; Koehl 1984). This observation seems

puzzling in light of the water currents and waves that seaweeds can withstand, until the toughness of algal tissues is considered. The amount of work that must be performed by moving water to break an alga depends on the toughness of the plant.

The area under the force-extension curve of a tissue pulled until it breaks represents the work required to break the specimen; a measure of a tissue's toughness is its work of fracture, the quantity of energy required to break a given cross section of the material. The algal tissues described in Figure 18.5 were all pulled until they broke. *Lessonia* stipe tissue was stronger than that of *Durvillaea* stipe or blade. However, *Durvillaea* blade tissue stretched farther before breaking than did tissue from *Durvillaea* or *Lessonia* stipes. The values for the work of fracture for these three types of tissues are not significantly different (Koehl 1979), and compared with other biomaterials, these particular algal tissues are relatively tough (Table 18.1). These tissues illustrate that there are several ways to be tough: An alga can be tough by having stiff, strong tissues like *Lessonia* stipe, but an alga can also be tough by having very stretchy tissues, even if those tissues are not strong, like *Durvillaea* blade (Koehl 1982, 1984). I do not mean to imply, however, that all such materials are tough. If a material is extremely stiff, the area under its force-extension curve can be small; an example of such a brittle material is glass. Similarly, if a tissue is stretchy but very weak, the area under its stress-extension curve can also be small.

One can speculate about the constraints on algae made of extensible, weak material rather than stiff, strong tissue. If a load is applied for a period of time long enough to stretch an alga's tissue to its maximum extension, the tissue will then break if the stress in it is greater than its strength. Therefore, one might predict that algae with extensible, weak tissues could survive at sites where flow forces on them are high only if the duration of high loads is brief (i.e., shorter than the time required to stretch them to their breaking lengths) and if the plants' tissues are resilient enough to bounce back to their undeformed shapes between pulses of high load. *Nereocystis* stipes are weak, but are extremely extensible (Koehl and Wainwright 1977). Recordings of water movement encountered by *Nereocystis* blades reveal that peak velocities last only a fraction of a second (Koehl 1984). Furthermore, *Nereocystis* stipes are extremely resilient (Koehl 1982), as predicted. One might also predict that extensible, but weak, algae would be less likely to survive storms (when the magnitude and duration of flow forces are higher than under non-storm conditions) than would stiff, strong seaweeds of similar toughness. This prediction seems to be borne out in the case of *Durvillaea* and *Lessonia*: Greater proportions of *Durvillaea* are ripped off the shore during winter storms than are *Lessonia*

(Santelices et al. 1980). One could further speculate that extensible, weak algae might grow rapidly and produce their propagules before seasonally predictable storms rip them off the substratum. Both *Nereocystis* (Foreman 1970; Nicholson 1970; Vadas 1972; Duncan and Foreman 1980) and *Durvillaea* (Santelices et al. 1980) show these characteristics, in contrast to stiff, strong plants like *Lessonia* that grow more slowly, take longer to reach the spore-producing stage, and live for several years (Santelices et al. 1980). Of course, both the biomechanics and the population dynamics of many more species of algae must be studied before we can assess the generality of these predictions about the habitats or life histories of algae whose tissues possess particular mechanical properties:

No matter how strong or tough an alga's tissues are, the plant will be ripped off the substratum by moving water if the adhesion of its holdfast to the substratum fails, or if the rock [or mussel (Dayton 1973; Paine 1979), dead barnacle, etc.] to which it has attached breaks. Surveys of seaweeds washed up on beaches reveal that such holdfast or substratum failure can be quite common (e.g., Koehl and Wainwright 1977; Witman and Suchanek 1984; M. Koehl unpublished data). A number of people have suggested that seaweeds that are flexible, that have coiled stipes, or that have highly extensible tissues deform before they transfer to their holdfasts the full load hitting their thalli (e.g., Koehl and Wainwright 1977; Kain 1979; Norton et al. 1981, 1982; Koehl 1984; M. Denny, unpublished data). Such morphological features that render plants good shock-absorbers can protect the holdfast-substratum attachment from high loads at sites subjected to short pulses of rapid water flow, such as wave-beaten shores.

One important aspect of the breakability of macroalgae concerning which little is known is fatigue fracture. Many materials, when subjected to repeated stresses that are too low to break them initially, will eventually fail (e.g., Andrews 1968), as a coat hanger does when bent back and forth repeatedly. Fatigue failure appears to be involved in the breakage of *Durvillaea* stipes, which accumulate cracks that enlarge as the plants are repeatedly pulled by waves (Santelices et al. 1980). What roles do tissue microarchitecture, growth, and repair play in the susceptibility of different algae to fatigue fracture?

Epiphytes have been reported to make the blades of giant kelp, *Macrocystis* species, more brittle than unfouled blades (Lobban 1978; Dixon, Schroeter, and Kastendiek 1981). However, the reductions in strength and toughness of fouled blades have not, to my knowledge, been measured, and the mechanisms responsible for this effect have not been elucidated.

The mechanical properties of algal tissues may affect their susceptibility to herbivores as well as to damage by moving water. For example, Padilla (1982) found that for certain limpet radulae, more force was required to rasp tissue from the deformable blades of *Iridaea cordata* than from the more "leathery" blades of *Hedophyllum sessile* or from the stiff calcified crusts of *Pseudolithophyllum* species. These surprising results warn against making assumptions about mechanical susceptibility to predation based on measures of the strengths of tissues that have been broken in a manner that is very different from the way in which they are attacked by the harvesting tools of specific herbivores. The mechanical properties that render algal tissues most effective at resisting the teeth of other herbivores (such as fish or sea urchins) remain to be studied.

Tradeoffs

Thus far, we have discussed ways in which the mechanical behaviors of macroalgae depend on their structures. However, a morphological feature that improves some aspect of the mechanical performance of a seaweed may worsen the alga's performance of some other function. We shall mention a few examples of such tradeoffs.

Tradeoff between drag reduction and photosynthesis

Many sessile animals and plants that make their living by extracting food or dissolved substances from the water around them have morphological features that increase the degree to which they interfere with the water flowing by them (Koehl 1982, 1984). We might expect that such organisms would bear larger flow-induced forces than would other organisms that interfere less with ambient currents.

The giant bull kelp of the northwest coast of North America, *Nereocystis luetkeana*, provides an example of a sessile organism that "compromises" between increasing and decreasing the effects that ambient currents exert on it. A *Nereocystis*, which generally lives in water 10 to 17 m deep, is attached to the substratum by a holdfast and has a long, slim stipe terminating in a gas-filled float that holds the blades (which can be up to 4 m long) near the water's surface (Abbott and Hollenberg 1976). *Nereocystis* can be found at sites exposed to nonbreaking waves or to rapid tidal currents, as well as at sites protected from both wave action and fast currents (Koehl 1984, unpublished data). The blades of plants from exposed sites are narrow and flat, whereas those of plants from protected sites are wider and have undulate (ruffled) edges (Figure 18.7) (M. Koehl and R. Alberte,

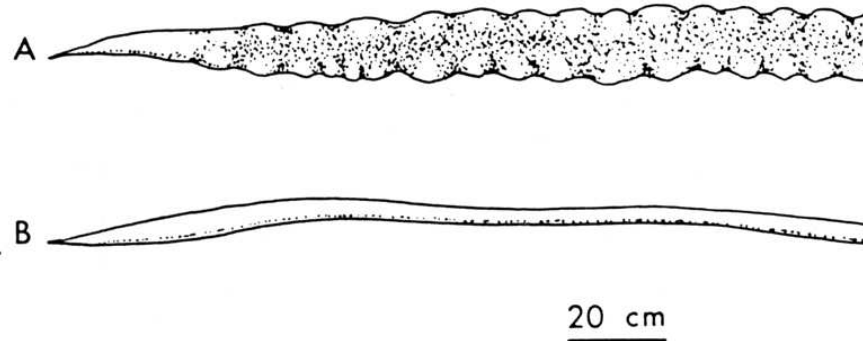


Figure 18.7. Proximal end of a blade of *Nereocystis luetkeana* from a site protected from rapid currents (A) and of *N. luetkeana* from a site exposed to rapid water flow (B) (drawings traced from photographs).

unpublished data). *Nereocystis* are flexible and stream out parallel to the direction of water flow, thereby reducing form drag, as described earlier. However, thin flexible structures such as algal blades flap in water currents as flags do in the wind. Such flapping increases the drag force on the blade (Hoerner 1965; Raupach and Thom 1981; Vogel 1981; Witman and Suchanek 1984).

The drag on *Nereocystis* with wide, undulate blades from protected habitats can be compared with the drag on *Nereocystis* with narrow, flat blades from exposed sites; the drag per blade area is about twice as large for the protected blades (M. Koehl and R. Alberte, unpublished data). Some of the increase in drag on protected plants is due to the undulate edges of their blades; the drag on a protected plant is greater than that on the same plant that has had its ruffled blades replaced by flat plastic models of its blades (Figure 18.8). However, the greater width of protected blades is also responsible for some of the increase in drag; the drag per blade area is greater for wide, flat models of protected blades than for real exposed blades, which are narrow and flat (M. Koehl and R. Alberte, unpublished data). Drag is higher on wide, undulate blades than on narrow, flat ones because the ruffled blades flap with greater amplitude than do the flat ones, and because the flat blades stack up on top of each other in skinnier streamlined bundles than do the undulate ones. If exposed *Nereocystis* had wide ruffled blades rather than narrow flat ones, and if the area of blades per plant was the same as that measured for exposed *Nereocystis*, the drag on the plants would be sufficient to break their stipes, even under non-storm conditions (M. Koehl and R. Alberte, unpublished data). Therefore, flatness and narrowness of blades could be considered morphological features that permit *Nereocystis* to attain large surface areas for photosynthesis at current-swept sites.

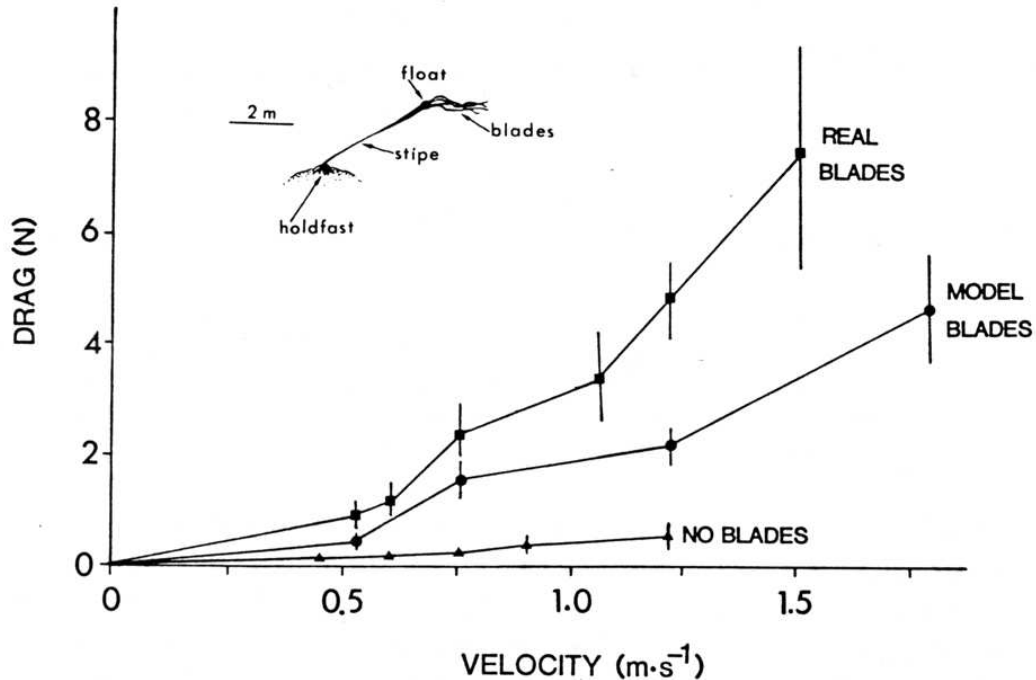


Figure 18.8. Drag force measured on a *Nereocystis luetkeana* (squares), on the stipe and pneumatocyst (float) after the fronds had been removed (triangles), and on the stipe and pneumatocyst plus plastic fronds (circles) (which were exact tracings of the removed fronds, but were flat rather than undulate). The alga was towed outside the wake of a boat, velocities were measured using an electromagnetic flow meter (EPCO water current meter, model 6130), and forces were measured using a spring dynamometer. Error bars represent one standard deviation. That this reduction in drag was due to lack of ruffles rather than to some other difference between real and plastic blades is supported by the observation that drag per blade area was greater for wide plastic blades than for narrow real blades (M. Koehl and R. Alberte, unpublished data).

Are there any advantages to plants bearing drag-increasing ruffled blades? R. Alberte and I (unpublished data) found that the photosynthetic rates of blades with undulate edges can be enhanced:

1. Algae take up bicarbonate to support photosynthesis and release dissolved organics and oxygen by diffusion. The boundary layer of slowly moving water along the surface of a blade can be thought of as a barrier across which diffusion, which can be the rate-limiting step in algal photosynthesis, takes place. Boundary layers are thinner and hence photosynthetic rates are higher the faster or more turbulent the flow across the surface of an alga; however, above some water-velocity saturation point, diffusion is no longer limiting to photosynthesis (Munk and Riley 1952; Whitford 1960; Whitford and Schumacher 1961, 1964; Schumacher and Whitford 1965; Westlake 1967; Conover 1968; Sperling and Grunewald

1969; Neushul 1972; Pasciak and Gavis 1974; Canelli and Fuhs 1976; Gavis 1976; Lock and John 1979; Smith and Walker 1980; Wheeler 1980a, 1980b; Wheeler and Neushul 1981; Anderson and Charters 1982; M. Koehl and R. Alberte, unpublished data). Alberte and I found that flapping, which is more pronounced for ruffled *Nereocystis* blades than for flat ones, stirs the water near blade surfaces and can nearly double photosynthetic rates in slow ambient currents such as protected *Nereocystis* often encounter. Other morphological features of algae that have been suggested as introducing turbulence near blade surfaces, and thus enhancing photosynthesis, include rugosities, perforations, marginal spines, and floats (which cause fronds to bounce up and down in waves) (Neushul 1972; Wheeler 1980a, 1980b; Norton et al. 1981; Gerard 1982).

2. Alberte and I found that ruffles can also enhance the photosynthesis of *Nereocystis* blades in water currents above saturation velocities. Undulate edges help prevent self-shading when blades are in moving water, not only by keeping the blades spread apart but also by increasing the amplitude and variability of blade motion such that the amount of time that one blade finds itself under another is reduced.

The advantages of wide ruffled blades carry with them the cost of increased drag forces to be sustained by stipes and holdfasts. It should not be surprising, therefore, that some macroalgae (such as *Hedophyllum sessile* and several species of *Laminaria*) have flat, narrow blades at current-swept sites, but undulate, wide blades at protected sites (e.g., Sundene 1964; Russell 1978; Gerard and Mann 1979; Kain 1979; Armstrong 1982). Whether or not the other structures (e.g., spines, rugosities) thought to enhance the movement of substances to algal surfaces also carry with them the cost of increased drag remains to be studied.

Tradeoff between unbreakability and photosynthesis

A number of people have suggested that a tradeoff exists for seaweeds between mechanical sturdiness and photosynthetic performance or productivity (e.g., Gerard and Mann 1979; Littler 1979; Littler and Littler 1980; Norton et al. 1981, 1982; Mann 1982; Littler et al. 1983). The investment of materials and energy in structural components means that less is available for producing photosynthetic machinery (or propagules). Furthermore, a large ratio of structural material to photosynthetic material in a thallus can cause internal self-shading. Similarly, the low surface-to-volume ratios of robust plants can limit the rates at which they take up nutrients from the surrounding water. However, plants with such investments in mechanical support can survive at wave-swept sites where the supply of dissolved substances by moving water is enhanced, where the

activity of herbivores may be restricted, and where other organisms that could otherwise out-compete these plants for space may be ripped away. A striking example of tradeoffs between the mechanical and photosynthetic performances of seaweeds of different shapes is provided by *Laminaria longicruris*, which is plastic in morphology (Gerard and Mann 1979). As described earlier, photosynthetic rates of algae can be increased by ambient water flow, as can growth rates (e.g., Matsumoto 1959; Boalch 1961; Whitford and Kim 1966; Norton et al. 1982). Nonetheless, *L. longicruris* shows higher growth rates at protected sites (where plants produce thin, wide, undulate blades) than at exposed sites (where plants have thick, narrow, flat blades, and where transplants from protected sites are torn apart by wave action) (Gerard and Mann 1979).

Conclusions

The distributions of various species and morphological types of seaweeds in different water-flow habitats have been extensively studied; see the reviews by Schwenke (1971), Neushul (1972), Mann (1973), Chapman and Chapman (1976), Russell (1978), and Norton et al. (1981, 1982). Furthermore, a number of cases of environmentally correlated within-species variations in seaweed morphology have been documented; see the reviews by Russell (1978), Kain (1979), Mathieson et al. (1981), Norton et al. (1981, 1982), and Mann (1982). One purpose of this chapter has been to illustrate that an engineering approach can be used to study, in a quantitative experimental manner, the ways in which such observed differences in morphology of macroalgae affect defined aspects of their mechanical performance in various water-flow habitats.

A second purpose of this chapter has been to advertise the field of algal functional morphology as one that offers a rich array of problems for which the sorts of quantitative optimization studies described elsewhere in this volume could be done. We have focused in this chapter on biomechanical analyses of ways in which the shapes of macroalgae and the mechanical properties of their tissues affect the flow forces they experience, their deformation and breakage in moving water, and their uptake of dissolved substances. Of course, the morphologies of seaweeds also affect their performance of other functions such as capturing light (e.g., Ramus 1978; Littler 1979; Littler and Littler 1980; Hay 1981a; Jeffrey 1981; Norton et al. 1981, 1982; Wheeler and Neushul 1981; Littler et al. 1983), resisting desiccation (e.g., Kristensen 1968; Hay 1981a; Norton et al.

1982), dispersing spores or sperm (e.g., Fetter and Neushul 1981; Norton et al. 1982), and resisting herbivores (e.g., Lubchenco 1978; Lubchenco and Cubit 1980; Slocum 1980; Dethier 1981; Hay 1981a, 1981b; Norton et al. 1982; Padilla 1982; Littler et al. 1983). Thallus designs that improve the performance of some of these functions appear to worsen the performance of others (e.g., Littler and Littler 1980).

A third purpose of this chapter has been to show that there are different morphological ways of performing a particular mechanical task, such as withstanding breaking waves. Furthermore, even plants with "bad" mechanical designs (such as drag-increasing shapes, or easily breakable tissues) can survive on wave-swept shores if they use the appropriate life-history "strategy." Of course, many biological interactions and physical factors affect the abundance and distribution of macroalgae of various morphologies. Nonetheless, I hope that the observations concerning seaweeds and the mechanical rules by which they operate that I have listed in this chapter will provide food for thought for those analyzing constraints on plant form and function.

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Appendix I: Notation

- A = cross-sectional area (m^2)
- C_D = coefficient of drag
- C_M = added-mass coefficient
- d = diameter of a cylinder (m)
- E = tensile elastic modulus of a tissue ($N\ m^{-2}$)
- F_D = drag force (N)
- F_I = acceleration reaction force (N)
- G = shear elastic modulus of a tissue ($N\ m^{-2}$)
- h = height of an organism
- I = second moment of area of a cross section of a bent organism (m^4)
- J = polar second moment of area of a cross section of a twisted organism (m^4)

- l = distance of a bit of tissue from the free end of a sessile organism (m)
 M = perpendicular distance between the point of load application and the axis of rotation of a twisted organism (m)
 S = characteristic area of a body (usually plan area, surface area, or projected area normal to the direction of water flow) (m^2)
 t = thickness of the wall of a hollow cylinder (m)
 U = velocity of water flow (m s^{-1})
 V = volume of an organism (m^3)
 y = distance of a bit of tissue from the axis of bending of a sessile organism (m)
 δ = linear deflection of the free end of a bent sessile organism (m)
 λ = extension ratio of a stretched piece of tissue (i.e., ratio of its extended length to its unstretched length)
 μ = viscosity of seawater ($1.39 \times 10^{-3} \text{ N s m}^{-2}$ at 10°C)
 ρ = density of seawater ($1.026 \times 10^3 \text{ kg m}^{-3}$ at 10°C)
 σ = tensile or compressive stress in an organism's tissues (N m^{-2})
 θ = angular rotation of the free end of a twisted sessile organism (rad)
 τ = shear stress in an organism's tissues (N m^{-2})

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