
Review

The mechanics of wave-swept algae

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Summary

Wave-swept marine algae must contend with the hydrodynamic forces imposed by extreme water velocities. Nonetheless, they seldom have a shape that appears streamlined and they are constructed of weak, compliant materials. How do they survive? The answer is complex, but a coherent story is beginning to emerge. The combined effect of frond shape and material properties ensures that algae are flexible. In small individuals, flexibility allows the plant to reorient and reconfigure in flow, thereby assuming a streamlined shape and reducing the applied

hydrodynamic force. In large individuals, flexibility allows fronds to ‘go with the flow’, a strategy that can at times allow the plant to avoid hydrodynamic forces but may at other times impose inertial loads. Our understanding of algal mechanics is such that we can begin to predict the survivorship of algae as a function of size, spatial distribution and wave climate.

Key words: marine alga, ocean wave, kelp, intertidal zone, hydrodynamic force, material properties, nearshore ecology.

Introduction

As large terrestrial organisms, it can be difficult for humans to grasp what it is like to live in the wave-swept environment of a rocky shore. For example, before waves break they are often accompanied by water velocities of 2 m s^{-1} (Denny, 1988), while velocities as high as 25 m s^{-1} have been recorded in the surf zone (M. W. Denny, unpublished data). But these dry facts have little impact on psyches accustomed only to the forces imposed by the wind. Perhaps the following analogy will help. The force imposed on a structure by a water velocity of 2 m s^{-1} is roughly equivalent to that exerted by a wind of 130 miles h^{-1} . In other words, the relatively gentle motions of unbroken ocean waves are equivalent to hurricane-force winds. If air were incompressible, a surf-zone water velocity of 25 m s^{-1} would exert a force equivalent to an air velocity of approximately 1600 miles h^{-1} , somewhat in excess of Mach 2. Because of the actual compressibility of air at high Mach numbers, this calculation must be taken as a rough estimate, but the message remains the same: to envision the challenge faced by an organism in the surf, one must imagine oneself strapped to the nose of a supersonic airplane. And these forces are not rare; waves crash on the shore every few seconds.

How are organisms designed to survive in these sorts of extreme environments? To put the question in the context of our analogy, how would the morphology of sylvan plants and animals have evolved if every 10 s or so a hurricane-strength breeze or a gust of supersonic wind roared through the forest? In most cases, the animals of wave-swept shores resemble what

one might intuitively expect – small, armored individuals firmly attached to the ground. A limpet, for instance, has a body contained within a rigid, streamlined shell and adheres to the rock’s surface with a relatively huge, glue-covered foot. A sea star has a body that can periodically be softened to conform to the shape of the substratum, but then hardens in place; the resulting armored structure is held down by hundreds of tube feet. In both cases, the organisms are quite small. As one might expect, collecting wave-swept animals is often a job requiring pry bars and chisels.

In contrast, wave-swept marine algae are a surprise. With few exceptions, they have eschewed the strong, stiff armor typical of nearshore sessile animals and are constructed instead of weak, compliant materials. Collecting marine algae is often simple – score a plant with a thumbnail and it practically falls off the rock. Furthermore, wave-swept algae occur in a myriad of shapes, few of which appear to be classically streamlined. The common morphological theme seems to be flexibility rather than protection, which (as we will see) can have both advantages and disadvantages. And, while many wave-swept algae are of a small size similar to that of the co-occurring animals, some (e.g. the giant kelp *Macrocystis pyrifera*) are quite large, reaching lengths of more than 30 m and masses in excess of 50 kg (Foster and Schiel, 1985).

How can we account for the non-intuitive design of wave-swept plants? In recent years, the general outline of a story has emerged that provides insight into how evolution has responded

to the exigencies of a uniquely stressful environment. This information may have practical utility in evaluating how these ecologically and economically important plants will respond to predicted changes in the wave climate of the ocean.

Algal morphology

Despite their morphological diversity, wave-swept macroalgae have a consistent basic body plan. The individual is attached to the substratum by a holdfast. Unlike the root of a terrestrial plant, the holdfast generally does not intercalate into the substratum and has no specialized structures for the absorption of water or nutrients. In some algae, the holdfast is discoid, in others it consists of a collection of fingerlike haptera. Extending from the holdfast is the stipe, a structure akin to the stem of a terrestrial plant. The stipe can be short to the extent that it is difficult to identify as a separate structure (as in the sea lettuce *Ulva*) or long enough so that it comprises most of the plant (as in the bull kelp *Nereocystis*). Attached to the stipe are blades, the primary photosynthetic organs of the plant. The blades can be attached along the entire length of the stipe or they may be confined to the stipe's distal end. The stipe and blades together are called a frond. In some species, there is a single frond per holdfast; in others, a single holdfast can anchor more than a hundred fronds.

As noted above, this basic body plan allows for an immense diversity of shapes (see, for example, Abbott and Hollenberg, 1976; Druehl, 2000). Some algae have no fronds and exist as a simple crust on the rock. Some have unbranched stipes, while others branch repeatedly. Blades may be simple, two-dimensional, strap-like sheets or complex, three-dimensional frills. In many of the large brown algae (in particular, many kelps), fronds may include one or more gas-filled floats termed pneumatocysts. These floats help to ensure that the blades are held as near as possible to the surface of the water, where light is most intense and photosynthesis is thereby enhanced.

Flexibility: the role of materials

With the prominent exception of the crustose forms (see, for example, Steneck, 1986), all wave-swept macroalgae are easily susceptible to being bent. In fact, at low tide when the plants are not buoyed by water, most wave-swept algae lie recumbent on the substratum. A few genera (such as *Laminaria*, *Pterygophora* and *Eisenia*) have so-called 'woody' stipes that are capable of resisting gravity and holding the plant upright, but these are the exceptions rather than the rule.

The flexibility of algal fronds is due in part to the properties of the materials from which the fronds are constructed. In general, both stipes and blades are made from materials that have a low stiffness and a high extensibility. Typically, stiffness (=elastic modulus, E) is within the range 1–100 MPa (a bit stiffer than rubber and less stiff than tendon), and these algal materials can be extended by more than 10% (a strain >0.1) before they break (Koehl, 1986; Denny et al., 1989; Hale, 2001). Even the 'woody' stipe materials are relatively compliant. For example, the stipe of *Eisenia* has a modulus of only 60 MPa (Gaylord and Denny, 1997), well below the stiffness of wood (10 000 MPa;

Wainwright et al., 1976). (Note that 'woody' algal materials contain no real wood; they have neither xylem nor phloem and their cell walls are not lignified.) Algal materials also differ from wood in that their stiffness in tension is often considerably higher than their stiffness in compression (Biedka et al., 1987; Holbrook et al., 1991; Gaylord and Denny, 1997). This often-overlooked feature has the potential to affect strongly the stress distributions developed in the tissues of some species (Gaylord and Denny, 1997). Coralline algae are characterized by calcified cell walls, and their materials can thereby be both stiff and inextensible. However, articulated (as opposed to crustose) corallines have uncalcified 'joints' (geniculae) in their fronds, which allow these plants to flex back and forth.

The energy per volume that a material can absorb before it breaks (strain energy density, J m^{-3}) is proportional to the product of the elastic modulus and the breaking strain. As a result, the low stiffness of algal materials tends to offset their high extensibility, and their strain energy density is typically within the range 0.1–1 MJ m^{-3} (Hale, 2001). This is 10- to 100-fold lower than that of materials such as collagen and the protein rubbers (elastin, abductin, resilin), and 100- to 1000-fold lower than that of mussel byssal threads and spider silk (Hale, 2001).

Algal materials have a low work of fracture (0.2–3 kJ m^{-2}) (Biedka et al., 1987; Denny et al., 1989; Hale, 2001) and, like all such materials, are susceptible to breakage by the propagation of small initial flaws. For example, a pane of glass is easily broken by first scoring it with a diamond stylus. Similarly, if one bends the stipe of a kelp and makes even a small cut at the outside of the bend, the stipe breaks catastrophically. This is the basis for the ease with which kelps can be collected, noted above. [Note that the work of fracture values reported in Biedka et al. (1987) and Denny et al. (1989) must be multiplied by 4 (Hale, 2001).]

Structural flexibility

The low stiffness of algal materials combines with the shape of the plant to yield the overall flexibility characteristic of these organisms. In general, the stipes and blades of wave-swept algae are rod-like or strap-like structures in which D , the smallest lateral dimension, is much less than the length of the organism, L . As a result, most seaweeds have cross sections with a relatively small second moment of area (a quantity proportional to D^4). The overall flexibility of the structure, the distance it deforms per force applied, is a combination of both its second moment of area (i.e. a function of its shape) and its material, varying in proportion to L^3/ED^4 (see Denny, 1988). Thus, the low modulus and small D of the stipe, coupled with the plant's relatively great length, ensure that it is easily bent. The stipe of the giant bull kelp *Nereocystis leutkeana* is an excellent example. The material has a modulus of approximately 50 MPa (Johnson and Koehl, 1994), only a little bit stiffer than cartilage. The stipe is circular in cross section with a diameter less than 1 cm along most of its length, while it can be more than 20 m long. As one can imagine, in its flexibility, this algal structure resembles a rope much more than it does the trunk of a tree.

The nearshore flow environment

Water motion along wave-swept coasts is dominated by the reciprocating flows associated with surface gravity waves as they move towards shore. The nature of these flows can be separated into two categories. If the height of a wave (H , the vertical distance from crest to trough) is less than approximately 80% of the local depth of the water column, d , the waveform moves in an orderly fashion and the water moves in nearly closed orbits. In contrast, when a wave reaches a depth such that $H > 0.8d$, it breaks, and the waveform subsequently propagates as a turbulent bore.

Flow prior to wave breaking

In unbroken waves, the pattern of flow (as predicted by linear wave theory) (Kinsman, 1965; Denny, 1988) is determined by the wave height, the depth of the water column and the wave period, T . The inter-relationship among these variables is complicated, but there are two points common to all waves. First, water particle velocity (as distinct from the velocity of the waveform) is directly proportional to wave height: the higher the wave, the faster the flow. Second, for any wave period, the shallower the water column, the higher the orbital speed (Fig. 1).

Fig. 1 also exposes two fundamental differences between flow at the surface and flow at the substratum. First, for a given wave period, as the water column gets deeper, flow at the surface asymptotes to a fixed, positive velocity (best seen for $T=5$ s in Fig. 1A) while, in contrast, flow at the substratum asymptotes to zero (see the line for $T=5$ s in Fig. 1B). In other words, if the water column is sufficiently deep (or the wave period sufficiently short), algae living near the sea floor can avoid wave-driven flows, whereas algae whose long stipes and buoyant pneumatocysts allow them to reach the water's surface must always contend with the waves. (Note that, although the water velocity at the surface is always greater than that at the seafloor, for water column depths less than approximately 5 m the difference is slight.) Second, for any water column depth, flow depends on the wave period. For flow at the substratum, the longer the wave period, the higher the velocity. For flow at the surface, the longer the wave period, the lower the velocity.

An example is perhaps in order. Ocean swells on exposed shores typically have a period of 10 s and a height of 2 m. Given these values and a water-column depth characteristic of giant kelps (20 m), the maximum velocity at the surface is 0.8 m s^{-1} , while at the substratum it is only 0.5 m s^{-1} . At a shallower depth near the point of breaking (2 m), the velocity at the surface has increased approximately fourfold to 2.3 m s^{-1} , a value that is nearly matched by that at the sea floor, 2.2 m s^{-1} .

The velocity imposed by an unbroken wave varies with position relative to the waveform – speed of flow is maximal under the crest and trough. However, given the large wavelengths typical of ocean waves (tens of meters) (see Eckart, 1952; Denny, 1988), the rate of spatial variation in velocity is small, and velocity is nearly constant along all but the longest fronds.

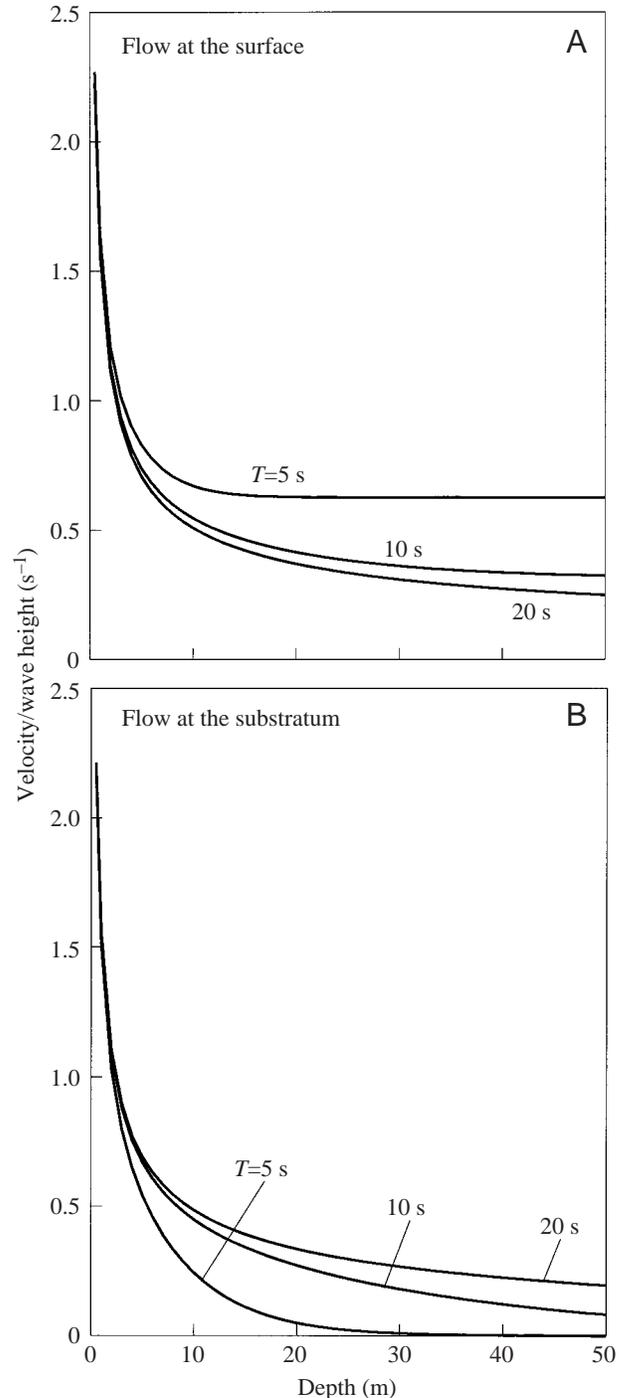


Fig. 1. Water velocities produced by unbroken surface gravity waves. In each case, velocity has been normalized to wave height so that these curves apply equally to waves of all heights. (A) Flows at the surface. (B) Flows just outside the benthic boundary layer at the seabed. T is wave period, in seconds. The depth referred to on the abscissa is the depth of the water column in the absence of waves.

The acceleration of water in an unbroken wave can be calculated from linear wave theory in a fashion similar to that for velocity (see, for example, Denny, 1988). However, these accelerations are small relative to those in broken waves

(typically less than 5 m s^{-2}), and their effects will not be explored here.

Although the orbital velocities imposed by unbroken waves dominate flow outside the surf zone, unidirectional currents can also be present, and these may affect algal dynamics. Two types of current are worthy of note. Subtle aspects of wave motion result in a slow transport of water in the direction of wave propagation (i.e. typically towards shore). This current (which usually amounts to at most a few cm s^{-1}) is known as Stokes drift (Kinsman, 1965; Denny, 1988). In addition, a number of oceanographic factors can result in a longshore current (Pond and Pickard, 1983). The speed of this current can vary widely over time and as a function of location, but is generally slow compared with orbital velocities.

Flow after wave breaking

Thus far, we have considered only the regular, predictable flows associated with currents and unbroken waves. These are the flows imposed on the giant kelps. However, as waves move inshore, become unstable and break, they degenerate quickly to produce the complex, highly energetic turbulence characteristic of a propagating bore, the type of flow imposed on algae in the surf zone. The rotating, stretching and twisting eddies associated with this complexity combine with the bulk movement of the bore itself to generate maximal flow speeds somewhat in excess of $(gH_b)^{1/2}$ (Denny, 1995; Gaylord, 1999), where g is the acceleration due to gravity and H_b is the height of the bore. As an example, a typical broken wave with an inshore height of 2 m will produce velocities somewhat in excess of 4.4 m s^{-1} , more than double that found in an unbroken wave of the same height. Topographic effects may then further funnel the flow locally to create the exceptionally large velocities (25 m s^{-1}) noted in the Introduction. Because there is only modest attenuation with vertical position within a broken wave and little time for a boundary layer to be established, these extreme surf-zone flows can impinge routinely even on algae whose blades are situated only a few millimeters above the substratum.

The spatial scales over which velocity is uniform within a turbulent bore range from a few centimeters to over a meter (Gaylord, 2000). These spatial scales are 1–2 orders of magnitude smaller than those associated with unbroken waves, but are still large enough to encompass substantial portions of most intertidal seaweeds. As a result, many moderately sized surf-zone plants will experience velocities as largely coherent flow fields along their lengths.

This is not the case for the fluid accelerations produced in bores, which are typically characterized by spatial scales of less than a centimeter (Gaylord, 2000). The forces imposed by these accelerating parcels of fluid vary in proportion to the volume of organism they enclose. As a direct consequence, although the magnitudes of the accelerations can be impressive (commonly hundreds of m s^{-2}) (Denny et al., 1985; Gaylord, 1999), their small spatial scales prevent them from interacting with a large enough portion of an alga to impose a dangerous force (Gaylord, 2000). This hydrodynamic subtlety appears to negate a number of expectations, based on standard fluid

theories, that fail to account for the restricted dimensions of the accelerations (e.g. Denny et al., 1985; Gaylord et al., 1994).

There is an additional fluid-dynamic phenomenon that occurs high in the surf zone. When macroalgae are emergent at low tide, arriving waves may crash directly against them. This leaves individuals with no interposed liquid cushion for protection. Recent field measurements indicate that the most severe forces applied to intertidal plants are often associated with such 'wave impingement' events (Gaylord, 2000; Gaylord et al., 2001). These large, but brief, forces arise intrinsically as a result of the requisite rapid evolution of a far-from-steady-state flow field as the free surface of a wave first encounters an organism (Gaylord, 2000).

Flow and survival

The fluid-dynamic forces imposed on nearshore macroalgae (see, for example, Fig. 2A–C) due to wave-driven flows are scaleable according to the size and shape of a plant. Thus, F , the largest of these forces (either drag or the impingement force, which varies in much the same way) can be modeled as:

$$F = \frac{1}{2} \rho u^\beta A C, \quad (1)$$

where ρ is the density of sea water (1025 kg m^{-3}), u is the water velocity relative to the plant and A is the maximum projected area of the frond(s). C is a coefficient whose magnitude depends on the shape of the organism and the manner in which force is imposed (Denny, 1995; Gaylord, 2000). Bluff objects (such as acorn barnacles or sea urchins) have large values of C ; streamlined objects have low values. When an impingement force is imposed, C can be 2–3 times the values associated with drag (Gaylord, 2000). The exponent β determines how force increases with an increase in imposed water velocity. For bluff objects subjected to drag, β is approximately 2 (Denny, 1995), as it is for objects of all shapes in the few cases in which impingement forces have been measured. For streamlined objects subjected to drag, β is less than 2 (Gaylord et al., 1994).

As noted previously, in the absence of flow, most nearshore algae are not noticeably streamlined. However, as a result of the structural flexibility of algal fronds, this impression can be misleading. In unidirectional flow, fronds bend in response to the applied force, and the plant reorients and rearranges passively in a manner that results in an overall streamlining (Koehl, 1984, 1986; Koehl and Alberte, 1988). As a consequence, β for wave-swept algae in flow is universally less than 2 (typically approximately 1.5), and values as low as 0.8–0.9 have been reported (Carrington, 1990; Bell, 1999; Gaylord et al., 1994; Gaylord, 2000). There seems to be little correlation between the still-water shape of an alga and its inflow value of either β or C . In other words, the flexibility of algae (due both to their basic body plan and to the compliance of their materials) allows fluid-dynamic forces to be decoupled from shape – in rapid, steady flows many wave-swept algae seem to be approximately equally streamlined.

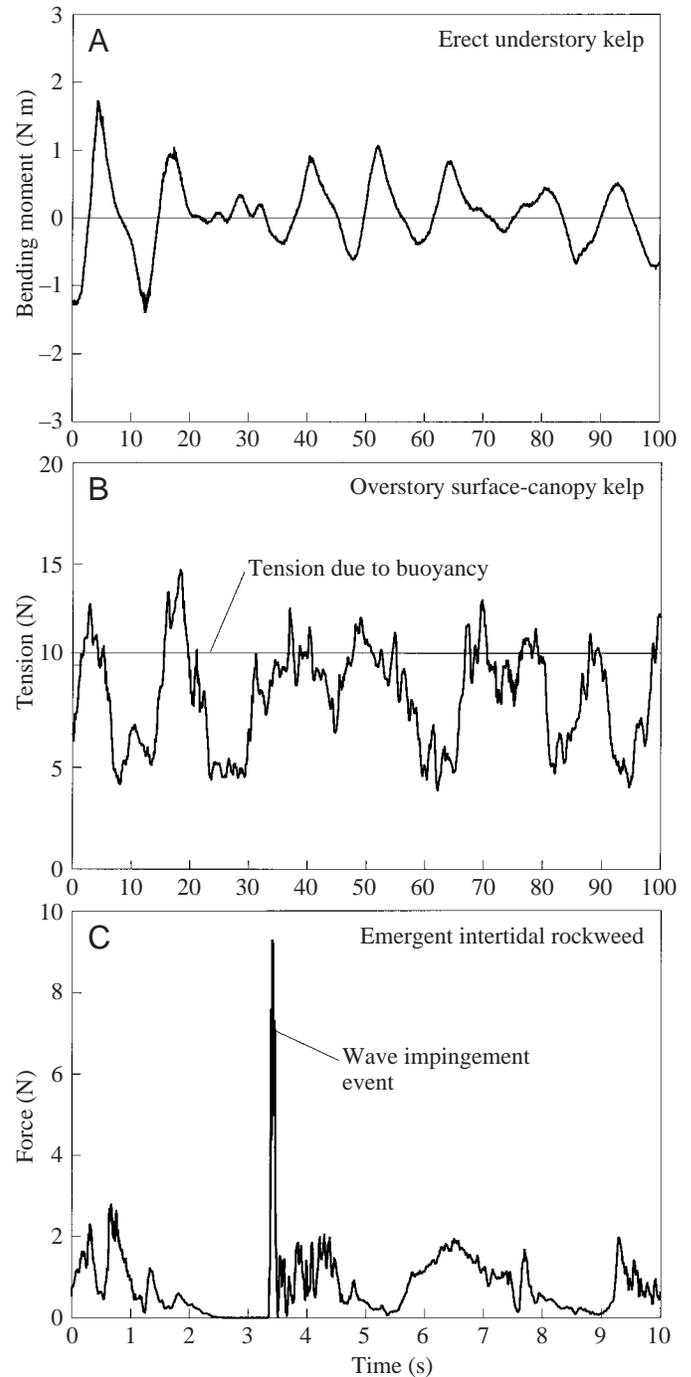
Fig. 2. Example time series of forces applied to seaweeds in the field. (A) Bending moments (i.e. forces applied with a given lever arm) imposed on the base of the stipe of an upright understory kelp *Pterygophora californica* exposed to unbroken waves. Note the relatively regular character of the recording. (B) Tensile force in a stipe of *Nereocystis luetkeana* exposed to unbroken waves. The slightly more complicated trajectory of force (which varies around that induced by the plant's buoyancy alone) probably arises from the seaweed's interaction with the water's surface as it is swept back and forth by drag. (C) A shorter time series of force applied to an emergent intertidal alga, *Pelvetia compressa*. The far more complicated fluid motions associated with wave impingement and breaking produce a rapidly evolving force record, particularly at the instant of wave arrival. Note that the magnitude of forces imposed on this small surf-zone plant (frond length 15 cm) rival those acting on the far larger (7 m length) subtidal bull kelp (compare B and C). This is a direct consequence of the greater severity of flow in intertidal regions.

Given this decoupling, the mechanical survival of a number of macroalgae subjected to drag or impingement forces is primarily a function of the interplay between maximum water velocity, frond area and the strength of either the stipe or holdfast (see, for example, Collado-Vides et al., 1998; Kawamata, 2001). For example, Carrington (1990) found that, while the frond area of the high intertidal red alga *Mastocarpus papillatus* increased throughout the plant's life, the stipe cross-sectional area (and with it the stipe's strength) remained constant. Setting F in equation 1 equal to the stipe's breaking strength, F_{br} , we can solve for the maximum frond area, A_{max} , as a function of imposed velocity:

$$A_{max} = \frac{2F_{br}}{\rho u^2 C} \quad (2)$$

The higher the imposed velocity, the smaller the fronds must be. Frond areas predicted in this fashion correspond closely to those measured in the field (Carrington, 1990; Bell, 1999).

The reproductive structures of *M. papillatus* are distributed over the fronds and, as a result, the plant's reproductive output is approximately proportional to frond area. Thus, because stipe strength is constant, the reproductive output of plants in areas of high flow is likely to be less than that in areas of low flow. The logic of this evolved life-history strategy becomes apparent only when we note that in this species many stipes emerge from a single, crustose holdfast. The strength of the stipes is low enough to ensure that the fronds (which can regrow) will detach before the holdfast (which is perennial) tears loose (Carrington, 1990). In 'good' times (a growing season without extreme water velocities), the fronds can reach a large size, and reproductive output is substantial; in 'bad' times (perhaps an early storm hits before spores can be released), the fronds (and potentially the individual's entire reproductive output) may be lost, but the holdfast persists to try again. These mechanics can lead to seasonal oscillations in blade size (Denny and Wethey, 2000). In an analogous scenario, differential mortality due to different scaling of blade area to stipe strength has been used to explain the pattern of coexistence in two intertidal algal species in



Maine (Dudgeon and Johnson, 1992). *Chondrus crispus* outgrows its neighboring *Mastocarpus stellatus* but, because it has larger blades for its holdfast strength, it is preferentially weeded out by winter storms. In general, disparities between applied hydrodynamic force and stipe or holdfast strength can be used to make quantitative predictions regarding habitat, life history or distributional patterns in algal species (e.g. Denny, 1995; Shaughnessy et al., 1996; Carrington et al., 2001; Kawamata, 2001).

Note that in some of these studies, however, calculations of applied hydrodynamic force have employed values for β based

on measurements made for $u < 5 \text{ m s}^{-1}$ and, thus, represent extrapolation well beyond the available data. Bell (1999) discusses the potential pitfalls of this extrapolation, but full resolution of the problem awaits drag measurements at higher velocities.

In contrast to the *Mastocarpus* and *Chondrus* discussed above, other species react to the imposition of dangerously high forces in a fashion that preserves at least part of the fronds. Blanchette (1997) has shown that, when transplanted from an area of slow flow to an exposed shore, the rockweed *Fucus gardneri* selectively 'tatters'. The overall area of the frond is reduced as distal sections break off, resulting in a 'pruned' plant of a size appropriate for its new environment.

Plant/flow relationships can also be modulated by other organisms. For example, numerous studies have documented the roles of grazers in undermining the structural integrity of macroalgal stipes (e.g. *via* fracture arising from sea urchin bites) (Koehl and Wainwright, 1977; DeWreede et al., 1992).

Interactions among multiple seaweed individuals in dense assemblages can also affect flow forces. For example, fronds of *C. crispus* may experience reduced forces as they recline against their neighbors (Johnson, 2001). It is also well recognized that individuals within a clump can 'hide' in the wake of upstream organisms (e.g. Eckman et al., 1989; Carrington, 1990; Johnson, 2001), employing an avoidance strategy similar to that used by plants compressing into the lower-velocity regions of substratum interstices (Koehl, 1984, 1986, 1999). In more extensive algal stands, even larger-scale flows may be diverted to pass around the periphery of an assemblage or attenuated within its interior (e.g. Fonseca et al., 1982; Jackson and Winant, 1983; Eckman, 1987; Gambi et al., 1990; Jackson, 1998). In yet other cases, propagating waves of deformation may pass through the canopy of understory algae as they bend synchronously to align with flow (Ackerman and Okubo, 1993).

Flexibility and dynamics

Passive reorientation has consequences beyond those associated simply with streamlining or deflecting into a more benign microhabitat. These consequences derive intrinsically from the dynamic motion of flexible macroalgae as they respond to the time-varying, bi-directional flows of the nearshore environment.

One of the more visible effects of reorientation is apparent in large subtidal species (e.g. *N. luetkeana* and *M. pyrifera*) that experience predominantly the simple flows of unbroken waves. These algae sway back and forth as waves pass by but, because of their great length, may only rarely be stretched out fully by a wave orbit before the flow reverses. This strategy of 'going with the flow' is therefore thought to result in a reduction of applied force (Koehl, 1984, 1986, 1999). There are additional complications, however, due to Stokes drift. Because this unidirectional component of flow acts along the direction of wave propagation, it has the potential to tug a plant to an extended position in which wave-driven velocities would impose force unabated. In other words, no matter how long the

stipe, it has a limited time in which it can go with the Stokes flow (see also Stevens et al., 2001). The critical issue then becomes whether a complementary longshore current is also present. By rotating the axis along which a plant is extended to an orientation more parallel with the coast, a longshore current may maintain an alga in a slack position with respect to the onshore/offshore orbits of the waves. In this way, a longshore current may ameliorate the tendency for Stokes drift to move the plant into a vulnerable orientation.

Although a critical field examination of the efficacy of going with the flow has not been conducted, there are some relevant data available for evaluating it. Measurements of flow damping within kelp beds in Southern California suggest, for example, that there is little attenuation of energy at the frequencies of ocean waves (Elwany et al., 1995). This finding supports the view that orbital velocities often do not apply substantial forces to large canopy-forming species, since otherwise the action of drag would result in a loss of this energy. Similarly, field measurements of tensile force in the stipe of a large *N. luetkeana* (Fig. 2B; Denny et al., 1997) showed that when wave heights were approximately 1 m, forces were small (only approximately 8 N in excess of buoyancy). Note that the strategy of going with the flow is unlikely to function as effectively in intertidal regions where bores often travel for tens of meters (many frond lengths) in the same direction before flow reversals occur, although some data suggest modest benefits (Koehl, 1999). This point, in conjunction with the augmented flow speeds found in the surf zone, may contribute to the expected capacity of wave breaking to set inshore boundaries to kelp beds (e.g. Seymour et al., 1989; Graham, 1997).

As the above discussions of algal reconfiguration and reorientation have indicated, there are a number of advantages to being flexible. However, there may also be some negative ramifications. One potential disadvantage derives from the momentum that seaweeds acquire as they move passively in flow. Because an attached alga has a finite range of motion, the plant's own mass can apply an 'inertial force' to itself as it decelerates at its furthest point of excursion (Denny et al., 1998). Under some circumstances, the component of force associated with momentum is predicted to outweigh any accompanying benefit due to going with the flow (Denny et al., 1997; Gaylord and Denny, 1997). Plants appear to be most vulnerable to this momentum effect when their natural periods of motion are near the dominant period of the arriving waves. This causes tuning between the external force and the dynamic response of the seaweed and essentially creates a plant/flow analogue to the so-called 'resonance' phenomenon often observed in simple spring-mass systems (Fig. 3; Denny et al., 1998). Other models predict additional, unfurling behaviors in some algae (e.g. the featherboa kelp *Egregia menziesii*) that may lead to superimposed whiplash (Friedland and Denny, 1995).

The fact that inertial forces due to momentum scale with mass may have consequences regarding the size of wave-swept algae. As described above, limits to the size of *M. papillatus*, *M. stellatus* and *C. crispus* exist because the forces of drag or wave impingement (proportional to frond area) increase out of

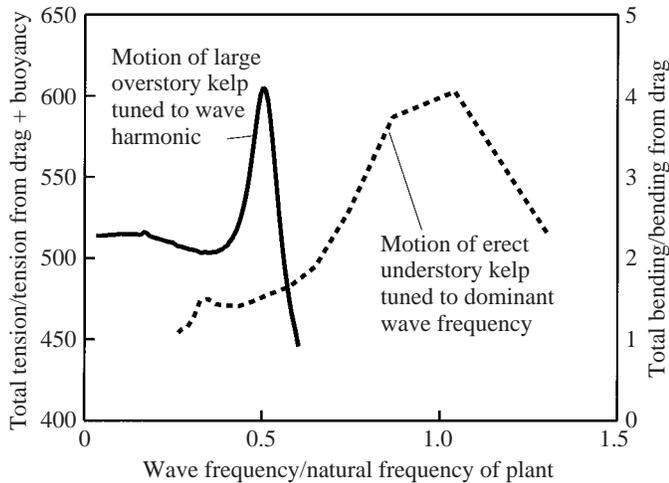


Fig. 3. Example model predictions of dynamic tuning in macroalgae subjected to unbroken waves showing how inertial effects can dominate applied force. In the case of the large surface-canopy kelp *Nereocystis luetkeana* (solid line and the ordinate on the left), peak tensile force (including forces due to the momentum the plant acquires as it moves) may occur when the waves arrive at a frequency equal to half the natural frequency of the seaweed, and these forces may greatly exceed the tensile force from drag alone. (The natural frequency is the frequency at which the plant would tend to oscillate if nudged slightly in still water.) Similarly, in an erect understory kelp, *Eisenia arborea* (dashed line and the ordinate on the right), total bending moments (i.e. moments including forces due to the momentum the plant acquires as it moves) may at times substantially exceed bending moments that would arise from drag alone. In this situation, the tuning is most apparent when the dominant frequency of the waves is the same as the natural frequency of the alga. Note that these model predictions assume a zero longshore current; if one is present, it may partially offset the exceptionally large tension ratios seen for *N. luetkeana*. In both curves, the magnitude of the orbital velocities produced by the waves is held constant across frequency. Denny et al. (1998) provide full details on this topic.

proportion to stipe strength. Large kelps (such as *N. luetkeana*), which go with the flow (and thereby possibly avoid these forces), could be immune to this effect. However, because factors that scale with mass are likely to increase more rapidly with increases in size than are factors that scale with area, this sets up a scenario in which, as a plant gets bigger, mass-dependent forces due to a seaweed's momentum could eventually come to exceed its area-dependent strength (Gaylord, 2000). This raises the possibility that motion allowed by flexibility in seaweeds places upper bounds on size (albeit less restrictive ones) even for the giant kelps. Further research will be required on this topic, however, before it can be viewed as anything other than conjecture.

Emerging evidence regarding the potential importance of wave impingement has exposed other potential limits to the functionality of a flexible body plan. Field recordings of impingement forces indicate that they last only a small fraction of a second (often less than 0.1 s; Fig. 2C) (Gaylord, 2000; Gaylord et al., 2001). Thus, for many seaweeds that reorient,

the peak of such a force pulse may have passed long before a plant can fully respond to it (Koehl, 1986; Denny, 1987; Gaylord, 2000). However, if an alga is already aligned with the direction of an impingement pulse when it is first applied, there may be a much reduced (or even nonexistent) capacity for amelioration of the effects of the pulse (Gaylord et al., 2001).

Future directions

Our understanding of the mechanics of algae in wave-swept flows, while still incomplete, nonetheless provides exciting opportunities for future interaction among fields of study. For example, laboratory experiments have shown that the shape in which wave-swept algae grow (Gerard, 1987) and the materials from which they are constructed (Kraemer and Chapman, 1991) respond to the forces imposed on the frond. An opportunity thus exists for a productive collaboration among the fields of plant developmental biology, fluid dynamics and materials science. Large areas of the world's oceans have become 'wavier' in recent years (Carter and Draper, 1988; Bacon and Carter, 1991; Hoozemans and Wiersma, 1992; Seymour et al., 1984; Seymour, 1996) in association with shifts in regional atmospheric gradients (Bacon and Carter, 1993) and the increase in frequency and severity of El Niño/Southern Oscillation events (Trenberth, 1993; Wellington and Dunbar, 1995). It is thus an opportune time for biomechanicians to collaborate with ecologists and climatologists to predict how the survivorship of marine algae may be affected by changes in wave intensity and, thereby, to predict an important component of the response of nearshore communities to changes in global climate.

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References

- Abbott, I. A. and Hollenberg, G. J. (1976). *Marine Algae of California*. Stanford, CA: Stanford University Press.
- Ackerman, J. D. and Okubo, A. (1993). Reduced mixing in a marine macrophyte canopy. *Funct. Ecol.* **7**, 305–309.
- Bacon, S. and Carter, D. J. T. (1991). Wave climate changes in the North Atlantic and North Sea. *Int. J. Climatol.* **11**, 545–558.
- Bacon, S. and Carter, D. J. T. (1993). A connection between mean wave height and atmospheric pressure gradient in the North Atlantic. *Inter. J. Climatol.* **13**, 423–436.
- Bell, E. C. (1999). Applying flow tank measurements to the surf zone: predicting dislodgement of the Gigartinales. *Phycol. Res.* **47**, 159–166.
- Biedka, R. F., Gosline, J. M. and DeWreede, R. E. (1987). Biomechanical analysis of wave-induced mortality in the marine alga *Pterygophora californica*. *Mar. Ecol. Progr. Ser.* **36**, 163–170.
- Blanchette, C. (1997). Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology* **78**, 1563–1578.
- Carrington, E. (1990). Drag and dislodgment of intertidal macroalgae:

- consequences of morphological variation in *Mastocarpus papillatus* Kützting. *J. Exp. Mar. Biol. Ecol.* **139**, 185–200.
- Carrington, E., Grace, S. P. and Chopin, T.** (2001). Life history phases and the biomechanical properties of the red alga *Chondrus crispus* (Rhodophyta). *J. Phycol.* **37**, 699–704.
- Carter, D. and Draper, L.** (1988). Has the north-east Atlantic become rougher? *Nature* **332**, 494.
- Collado-Vides, L., DeWreede, R. E. and Milligan, K. L. D.** (1998). Biomechanical properties of *Udotea* (Halimedales, Chlorophyta) in a Mexican reef lagoon. *Phycologia* **37**, 443–449.
- Denny, M. W.** (1987). Life in the maelstrom: the biomechanics of wave-swept rocky shores. *Trends Ecol. Evol.* **2**, 61–66.
- Denny, M. W.** (1988). *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, NJ: Princeton University Press.
- Denny, M. W.** (1995). Predicting physical disturbance: Mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* **65**, 371–418.
- Denny, M., Brown, V., Carrington, E., Kraemer, G. and Miller, A.** (1989). Fracture mechanics and the survival of wave-swept macroalgae. *J. Exp. Mar. Biol. Ecol.* **127**, 211–228.
- Denny, M. W., Daniel, T. L. and Koehl, M. A. R.** (1985). Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**, 69–102.
- Denny, M. W., Gaylord, B. P. and Cowen, E. A.** (1997). Flow and flexibility. II. The roles of size and shape in determining wave forces on the bull kelp *Nereocystis luetkeana*. *J. Exp. Biol.* **200**, 3165–3183.
- Denny, M. W., Gaylord, B., Helmuth, B. and Daniel, T. L.** (1998). The menace of momentum: Dynamic forces on flexible organisms. *Limnol. Oceanogr.* **43**, 955–968.
- Denny, M. and Wethey, D.** (2000). Physical processes that generate patterns in marine communities. In *Marine Community Ecology* (ed. M. D Bertness, S. D. Gaines and M. E. Hay), pp. 3–37. Sunderland, MA: Sinauer.
- DeWreede, R. E., Ewanchuk, P. and Shaughnessey, F.** (1992). Wounding, healing and survivorship in three kelp species. *Mar. Ecol. Prog. Ser.* **82**, 259–266.
- Druehl, L. D.** (2000). *Seaweeds: A Guide to the Common Seaweeds of the West Coast*. Madeira Park, British Columbia, Canada: Harbour Publishing.
- Dudgeon, S. R. and Johnson, A. S.** (1992). Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgment of two co-dominant seaweeds. *J. Exp. Mar. Biol. Ecol.* **165**, 23–43.
- Eckart, C.** (1952) The propagation of waves from deep to shallow water. In *Gravity Waves*, Circular No. 521, pp. 165–173. National Bureau of Standards, USA.
- Eckman, J. E.** (1987). The role of hydrodynamics in recruitment, growth and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J. Exp. Mar. Biol. Ecol.* **106**, 165–191.
- Eckman, J. E., Duggins, D. O. and Sewell, A. T.** (1989). Ecology of understory kelp environments. I. Effects of kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. Ecol.* **129**, 173–187.
- Elwany, M. H. S., O'Reilly, W. C., Guza, R. T. and Flick, R. E.** (1995). Effects of Southern California kelp beds on waves. *J. Waterway Port Coast. Ocean Eng.* **121**, 143–150.
- Fonseca, M. S., Fisher, J. S., Zieman, J. C. and Thayer, G. W.** (1982). Influence of the seagrass, *Zostera marina* (L.), on current flow. *Estuar. Coast. Shelf Sci.* **15**, 351–364.
- Foster, M. S. and Schiel, D. R.** (1985). The ecology of giant kelp forests in California: A community profile. *Biol. Rep.* **85**. U.S. Fish and Wildlife Service.
- Friedland, M. T. and Denny, M. W.** (1995). Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp *Egregia menziesii* (Turner). *J. Exp. Mar. Biol. Ecol.* **190**, 109–133.
- Gambi, M. C., Nowell, A. R. M. and Jumars, P. S.** (1990). Flume observations of flow dynamics in *Zostera marina* (eelgrass) beds. *Mar. Ecol. Prog. Ser.* **61**, 159–169.
- Gaylord, B.** (1999). Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. *J. Exp. Mar. Biol. Ecol.* **239**, 85–124.
- Gaylord, B.** (2000). Biological implications of surf-zone flow complexity. *Limnol. Oceanogr.* **45**, 174–188.
- Gaylord, B., Blanchette, C. A. and Denny, M. W.** (1994). Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* **64**, 287–313.
- Gaylord, B. and Denny, M. W.** (1997). Flow and flexibility. I. Effects of size, shape and stiffness in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora californica*. *J. Exp. Biol.* **200**, 3141–3164.
- Gaylord, B., Hale, B. B. and Denny, M. W.** (2001). Consequences of transient fluid forces for compliant benthic organisms. *J. Exp. Biol.* **204**, 1347–1360.
- Gerard, V. A.** (1987). Hydrodynamic streamlining of *Laminaria saccharina* Lamour in response to mechanical stress. *J. Exp. Mar. Biol. Ecol.* **107**, 237–244.
- Graham, M. H.** (1997). Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey peninsula, central California, USA. *J. Exp. Mar. Biol. Ecol.* **218**, 127–149.
- Hale, B. B.** (2001). Materials properties of marine algae and their role in the survival of plants in flow. PhD thesis, Stanford University.
- Holbrook, N. M., Denny, M. W. and Koehl, M. A. R.** (1991). Intertidal 'trees': consequences of aggregation on the mechanical and photosynthetic properties of sea-palms *Postelsia palmaeformis* Ruprecht. *J. Exp. Mar. Biol. Ecol.* **146**, 39–69.
- Hoozemans, M. J. and Wiersma, J.** (1992). Is mean wave height in the North sea increasing? *Hydrographic J.* **63**, 13–15.
- Jackson, G. A.** (1998). Currents in the high drag environment of a coastal kelp stand off California. *Cont. Shelf Res.* **17**, 1913–1928.
- Jackson, G. A. and Winant, C. D.** (1983). Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* **20**, 75–80.
- Johnson, A. S.** (2001). Drag, drafting and mechanical interactions in canopies of the red alga *Chondrus crispus*. *Biol. Bull.* **201**, 126–135.
- Johnson, A. S. and Koehl, M. A. R.** (1994). Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: thallus allometry and material properties of a giant kelp. *J. Exp. Biol.* **195**, 381–410.
- Kawamata, S.** (2001). Adaptive mechanical tolerance and dislodgement velocity of the kelp *Laminaria japonica* in wave-induced water motion. *Mar. Ecol. Prog. Ser.* **211**, 89–104.
- Kinsman, B.** (1965). *Wind Waves*. Englewood Cliffs, NJ: Prentice Hall.
- Koehl, M. A. R.** (1984). How do benthic organisms withstand moving water? *Am. Zool.* **24**, 57–70.
- Koehl, M. A. R.** (1986). Seaweeds in moving water: form and mechanical function. In *On the Economy of Plant Form and Function* (ed. T. J. Givnish), pp. 603–634. Cambridge: Cambridge University Press.
- Koehl, M. A. R.** (1999). Ecological biomechanics of benthic organisms: life history, mechanical design and temporal patterns of mechanical stress. *J. Exp. Biol.* **202**, 3469–3476.
- Koehl, M. A. R. and Alberte, R. S.** (1988). Flow, flapping and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies. *Mar. Biol.* **99**, 435–444.
- Koehl, M. A. R. and Wainwright, S. A.** (1977). Mechanical adaptations of a giant kelp. *Limnol. Oceanogr.* **22**, 1067–1071.
- Kraemer, G. P. and Chapman, D. J.** (1991). Biomechanics and alginic acid composition during hydrodynamic adaptation by *Egregia menziesii* (Phaeophyta) juveniles. *J. Phycol.* **27**, 47–53.
- Pond, S. and Pickard, G. L.** (1983). *Introductory Dynamical Oceanography*. Second edition. New York: Pergamon.
- Seymour, R. J.** (1996). Wave climate variability in southern California. *J. Waterway Port Coast. Ocean Eng.* **122**, 182–186.
- Seymour, R. J., Strange, R. R., Cayan, D. R. and Nathan, R. A.** (1984). Influence of El Niños on California's wave climate. In *Proceedings of the 19th Coastal Engineering Conference*. ASCE, September 3–7, 1984, Houston, TX, **1**, 577–592.
- Seymour, R. J., Tegner, M. J., Dayton, P. K. and Parnell, P. E.** (1989). Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Est. Coast. Shelf Sci.* **28**, 277–292.
- Shaughnessy, F. J., DeWreede, R. E. and Bell, E. C.** (1996). Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Mar. Ecol. Prog. Ser.* **136**, 257–266.
- Steneck, R. S.** (1986). The ecology of coralline algal crusts. *Annu. Rev. Ecol. Syst.* **17**, 273–303.
- Stevens, C. L., Hurd, C. L. and Smith, M. J.** (2001). Water motion relative to subtidal kelp fronds. *Limnol. Oceanogr.* **46**, 668–678.
- Trenberth, K. E.** (1993). Northern hemisphere climate change: physical processes and observed changes. In *Earth System Responses to Global Changes: Contrasts between North and South America* (ed. H. A. Mooney, E. R. Fuentes and B. I. Kronberg), pp. 35–39. New York: Academic Press.
- Wainwright, S. A., Biggs, W. D., Currey, J. D. and Gosline, J. M.** (1976). *Mechanical Design in Organisms*. London, UK: Edward Arnold.
- Wellington, G. M. and Dunbar, R. B.** (1995). Stable isotope signature of El Niño–Southern Oscillation events in eastern tropical Pacific reef corals. *Coral Reefs* **14**, 5–25.