

## CONSEQUENCES OF TRANSIENT FLUID FORCES FOR COMPLIANT BENTHIC ORGANISMS

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### Summary

**The diversity of form among benthic marine plants and animals on rocky coasts is remarkable. Stiff and strong organisms grow alongside others that are compliant and flimsy. Given the severity of wave action on many shores and thus the potential for the imposition of large hydrodynamic forces, this immediately raises the question of how, from this overall spectrum of designs, flexible and weak organisms survive. A number of explanations have been proposed, most emphasizing one or more of several possible advantages of deformability. Here, we explore quantitatively two of the more common of these**

**explanations: (i) that strength can be traded against extensibility in allowing stretchy organisms to withstand transient wave forces, and (ii) that greater compliance (and thus longer organism response times) allows universally for the amelioration of brief loads. We find that, although these explanations contain kernels of validity and are accurate for a subset of conditions, they are not as general as has often been assumed.**

Key words: hydrodynamic force, transient fluid force, benthic organism, compliance, wave action, macroalgae, seaweed.

### Introduction

The mechanical properties of biological structures and their materials are among the most fundamental of the numerous factors that dictate how plants and animals survive in their environment. An elephant could not stand on legs of mucin, nor could a fish swim with an integument of ivory. Such extreme examples are so obvious as to appear absurd. However, in many cases, the precise implications of strength, stiffness or the viscous characteristics of an organism's construction may be more difficult to discern. For example, the intertidal zone of rocky coasts is characterized by the routine imposition of large hydrodynamic forces, which might be expected to place strong constraints on material properties and morphology. Nevertheless, intertidal plants and animals embrace an extraordinarily wide range of structural and mechanical options.

Much of the apparent freedom of intertidal organisms to exhibit a diversity of form has been attributed to the presumed equivalent effectiveness of two quite different strategies: being both stiff and strong (as are barnacle tests, for example) or being highly extensible (like seaweeds). This general idea, which has reached near-paradigm status in the marine ecological literature, has been based on the observation that stretchy materials can be much weaker than stiffer materials yet still absorb as much energy before breaking (Koehl, 1982; Koehl, 1984; Koehl, 1986; Johnson and Koehl, 1994). Thus, if it is the energy of the system that determines the forces acting on organisms, plants and animals can trade strength against

extensibility in coping with those forces. This concept has functioned as a standard argument in attempts to explain how relatively weak and flimsy surf-zone organisms nonetheless manage to survive large forces imposed by breaking waves. We, for example, have made such remarks in recent work (e.g. Gaylord and Denny, 1997).

Unfortunately, although this explanation is grounded in proper physics, a more critical evaluation suggests that it can be misleading when applied to coastal benthic organisms. The difficulty arises from the implicit assumption that energy constrains the loading. While such may indeed be the case for a falling rock climber jerked to a halt by a safety rope, where the climber's kinetic energy and the rope's stiffness determine the rate of deceleration and thus the peak force, this situation differs from that encountered when forces are applied by flow. In the surf zone, for instance, only a negligible portion of the energy associated with any passing wave is absorbed by a given organism. As a result, the magnitude of applied force is not, in practice, limited by the amount of energy available; it is dictated, rather, by local hydrodynamic interactions between the plant or animal and the water moving past it.

The implications of this distinction can be important. Under conditions in which a fixed amount of energy controls the loading regime, peak force and peak deformation are always inversely related. Because the energy expended doing work equals the integral of force through distance, a larger force can be applied only if the maximum deformation decreases. In

contrast, in the surf zone, where the magnitude of force is set by hydrodynamics (i.e. where the energy of deformation is effectively no longer constrained), it is possible for large forces to be imposed on organisms of any degree of stretchiness. The apparent benefits of extensibility, as rationalized by simple energy arguments and as applied to wave-swept plants and animals, therefore become obscured.

This conclusion resurrects the question of how weaker organisms such as seaweeds do, in fact, manage to survive in the stressful arena of the surf zone. At least two other related, but subtly different, classes of mechanism have been proposed. First, lower stiffness and higher extensibility can alter the magnitudes of applied loads by changing the way in which organisms interact with flow. Intertidal plants, for example, passively reorient and reconfigure, reducing drag (Carrington, 1990; Gaylord et al., 1994), and it has been suggested that long kelps in oscillatory flows avoid large relative water velocities by swaying with the fluid during portions of each cycle (Koehl, 1982; Koehl, 1984; Koehl, 1986). Similarly, erect seaweeds in deeper waters may reduce moment arms and peak bending loads by deflecting towards the substratum in response to horizontal forces (Charters et al., 1969; Gaylord and Denny, 1997). Byssal extensibility in mussels may reduce the maximum forces borne by individual threads by allowing isolated tethers to stretch until others come into play (Bell and Gosline, 1996). Additional examples abound (e.g. Koehl, 1977; Patterson, 1984; Harvell and LaBarbera, 1985; Sponaugle and LaBarbera, 1991; Johnson, 1993; Vogel, 1994).

Such benefits reflect primarily the capacity of organismal compliance to affect the magnitudes of forces as they are being applied. In addition, another class of mechanism can modulate the deformations induced by a given force. Because compliant plants and animals must stretch farther than stiffer organisms for internal stresses to balance an externally applied load, and because this stretching takes time, full deformation may not be attained before a short, transient force is removed. Two components interact to cause this effect. First, because the mass of an organism must be accelerated before substantial deformation can ensue, a brief load may be expended almost entirely in overcoming inertia. It has commonly been assumed that this inertial hurdle ameliorates the consequences of many of the brief forces that act on flexible plants and animals in the surf zone (Koehl, 1984; Koehl, 1986; Denny et al., 1985; Denny, 1987; Johnson and Koehl, 1994; Gaylord, 2000). Unfortunately, this phenomenon has not been fully explored in a quantitative fashion, leaving the biological relevance of the concept unclear.

A second attribute that may alter the consequences of transient loads is the viscous component of the material properties of plants and animals, a trait that causes so-called 'retardation' (simplicistically, a lag) in the deformation response to an applied force. Koehl (Koehl, 1984) has pointed out that such viscous behavior can increase the effective structural rigidity of an organism subjected to a transient load. This is equivalent to noting that viscosity can reduce

the maximum deformations induced in plants or animals by brief forces, a phenomenon that may work to partially counter some of the reorientation and reconfiguration processes noted above.

Given the complexity of these issues linking stiffness, extensibility, strength, viscous characteristics and response to transient loads, we believe that a careful reconsideration of the basic principles is in order. We address two specific points here. First, we outline in further detail the problem with assuming that constraints on energy dictate the loading regime of benthic marine organisms (common misconception 1, see below). Second, we provide a general, quantitative exploration of the importance of inertia and viscous damping for two classes of simplified organism – those with relatively uniform distributions of mass along their lengths that bear applied forces primarily in tension, and those with relatively uniform distributions of mass that bear forces in bending – subjected to very brief loads. The goal here is to examine more closely the assumption that longer response times in organisms always ameliorate the effects of transient forces (common misconception 2, see below).

This approach assists primarily in clarifying the fundamental tenets of the response of compliant organisms to transient loads. Concomitantly, it may also serve to improve our understanding of the consequences of the exceptionally brief forces associated with the impingement of breaking waves on emergent plants and animals, a phenomenon that has recently been recognized as perhaps the most dangerous loading scenario operating in the surf zone of rocky coasts.

### Common misconception 1: energy trade-offs limit fluid forces

If one considers the balance of forces acting on a benthic plant or animal in flow, it is apparent that those forces can be separated into three major components. The first encompasses all the external loads pushing or pulling on an organism. These external forces are then counteracted (or modulated) by the other two components: the organism's inertia, and the internal elastic or viscous mechanisms operating within the tissues of the plant or animal that resist its deformation.

It is here that the difficulty arises in assuming that the energy of the system dictates the applied force, because such an assumption allows for a realistic accounting of only two of the three above components. To see why this is so, we consider a simplified, idealized organism of mass,  $m$ , attached to the substratum by an elastic organ (e.g. a stalk, stipe or appendage) that exhibits stiffness,  $k$ . In this situation, the three force components are related through the following equation which describes the organism's motion:

$$F_{\text{external}} = m \frac{d^2\xi}{dt^2} + k\xi, \quad (1)$$

where  $F_{\text{external}}$  is the applied force,  $\xi$  is the displacement of the organism's mass (acting to stretch its attachment organ)

and  $t$  is time. The left-hand side quantifies the external force, and the first and second terms on the right-hand side represent organism inertia and the elastic restoring forces associated with the extension of the organism's 'tether', respectively.

The solution to equation 1 depends on the magnitude of the external force and how it varies through time. However, if we ignore for the moment any externally applied loads to make the left-hand side zero, we find that the resulting equation has the form of a simple harmonic oscillator, which exhibits sinusoidal motion (see, for example, Ohanian, 1985). If the organism has initial velocity,  $U$ , at zero displacement, then it oscillates according to:

$$\xi = U \sqrt{\frac{m}{k}} \sin \sqrt{\frac{k}{m}} t. \quad (2)$$

As the organism moves back and forth, its maximum extension,  $\xi_{\max}$ , occurs when the sine term in equation 2 equals 1. The maximum force applied to the tether,  $F_{\max}$ , equals  $k\xi_{\max}$ . Thus:

$$F_{\max} = U \sqrt{km}. \quad (3)$$

That is, reducing the stiffness reduces the maximum force.

What is important about this equality here, however, is that it has the same form as the expression we would derive under the assumption that a particular parcel of kinetic energy,  $\frac{1}{2}mU^2$ , is converted into and determines the elastic energy of deformation,  $\frac{1}{2}k\xi_{\max}^2$  (calculated as the integral of the force/extension curve; see, for example, Gere and Timoshenko, 1990), induced within an organism as it stretches. In this situation (i.e. when energy constrains the loading), the kinetic and deformation energies equal each other, and we can solve for  $k\xi_{\max}$  as before to estimate the maximum force applied to the organism's tether. Once again, we regain an expression that resembles equation 3. However, recall that, in deriving equation 3, we completely ignored all details of the external forcing. The fact that we achieve the same result here reveals, therefore, that the assumption that a specifiable unit of kinetic energy sets the peak deformation and load disregards entirely what are likely to be important fluid dynamic factors influencing total imposed force.

Although such a simplification may be appropriate in specific situations (such as for the falling climber mentioned earlier), it will not be generally valid for organisms in flow. Indeed, if we explicitly and realistically model all three force components in equation 1, we find that lower stiffness can at times actually increase rather than decrease the total force that acts on benthic marine plants and animals (Denny et al., 1997; Denny et al., 1998; Gaylord and Denny, 1997). This contrasts with the more commonly accepted prediction embodied by expressions of the form of equation 3 in which the maximum force rises monotonically with increases in stiffness. In short, we find that arguments based solely on energy trade-offs are too simple to capture important aspects of the loading regimes of organisms in aquatic environments.

### Common misconception 2: longer organism response times always ameliorate brief loads

Given the above difficulties with traditional qualitative arguments regarding trade-offs between strength and extensibility in flow-dominated organisms, we turn now to a consideration of the related (and often accompanying) argument that flexible marine plants and animals ameliorate brief loads by having long response times (=long natural periods of motion). We examine this more complicated issue in three steps. First, we outline the essential physical characteristics of what are likely to be the briefest and largest forces imposed on many intertidal organisms. Second, we describe measurements of the relevant material properties of seaweeds, which we use as examples of compliant benthic organisms in general. And finally, we present results from numerical experiments, in which idealized, simple model organisms are loaded by pulsatile forces, either in tension or in bending, to examine the consequences of differences in material properties and gross morphology. We find once again that overly simplistic arguments can be misleading. Although flexible organisms may indeed experience attenuation of the effects of transient forces under some conditions, this is not necessarily a general outcome. Rather, the outcome can depend fundamentally on the way in which a plant or animal is loaded and the extent of tuning between the time course of the force and the natural frequency of movement of the organism.

#### Surf-zone forces

Of primary importance for intertidal plants and animals experiencing transient loads are the effects of the direct impingement of crashing waves on emergent organisms on the shore. Recent data suggest that such forces may include many of the most severe loads typically encountered (Gaylord, 1999; Gaylord, 2000). An example of a field recording of forces imposed by a breaking wave on a 1 cm diameter spherical force sensor is shown in Fig. 1A. These data demonstrate the rapidly varying nature of wave forces over time and the overwhelming dominance of the initial force spike (for technical details of the sensor and measurement techniques, see Gaylord, 1999). Fig. 1B presents an enlarged view from Fig. 1A of the region of initial impingement of the wave. This graph indicates the exceptionally brief durations of such impingement pulses (this particular example lasts only 0.08 s, for instance). Fig. 2 generalizes to show a histogram of field-recorded impingement force duration from approximately 70 waves, demonstrating that pulses with durations as short as or shorter than 0.05 s are common.

#### Material properties of seaweeds

The mechanical properties of the tissues of organisms can be quantified in a number of ways, but are perhaps most easily described in terms of two basic parameters, an elastic modulus ( $E$ ) and a loss modulus ( $E_{\text{loss}}$ ). The first parameter represents a material's stiffness, while the second represents its viscous character (for a more complete discussion of these quantities, see Ferry, 1980). In general, both properties vary as a function

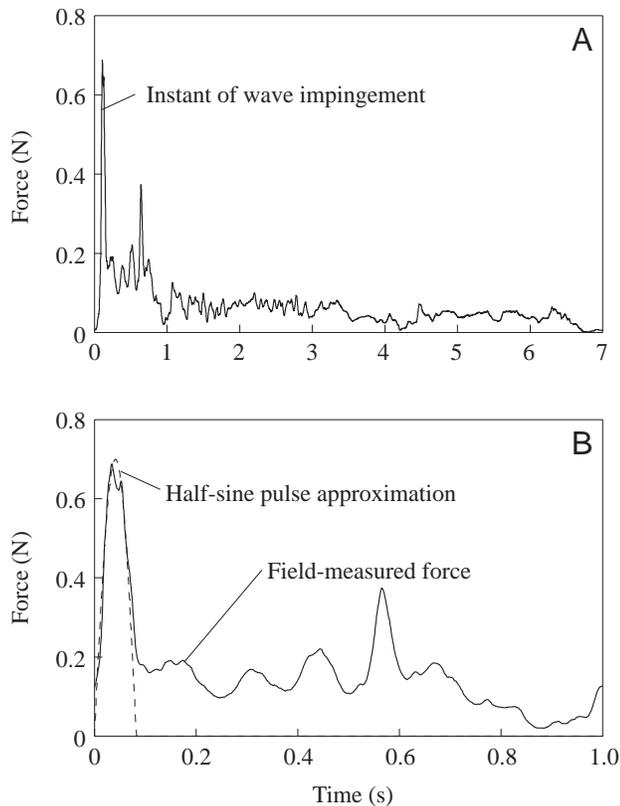


Fig. 1. Example of a force trajectory produced as a wave breaks on a rocky shore. (A) Forces through an entire wave, showing the characteristic rapid fluctuations and the large spike at the instant of wave arrival. (B) Expanded view of the first 1 s from A. The positive half of a sine curve (dashed line) provides a close approximation to the actual trajectory of the impingement pulse. Note that forces acting on larger organisms or applied by bigger waves can exceed substantially the values shown here.

of the time scale over which they are measured. Because of this, they are traditionally determined by deforming a tissue sample at a wide range of forcing frequencies, the approach taken here. A full description of the techniques employed is given by Hale (Hale, 2001) and is sketched again here as follows.

Algal samples were collected at Hopkins Marine Station, Pacific Grove, California, USA, and inserted fresh into the dynamic testing apparatus of Lillie and Gosline (Lillie and Gosline, 1996). This apparatus stretches samples between two grips at multiple frequencies. Each specimen was prestrained to approximately 10% and held at this extension until the resulting tension stabilized (approximately 3 min). The prestrain was used to ensure that samples did not become slack during testing. Deformations were subsequently induced in each sample by driving one grip of the testing machine *via* an electromagnetic vibrator. This vibrator is controlled by a function generator that creates random motion (band-limited white noise) with maximum displacements of approximately  $\pm 0.15$  mm. In the test pieces used, this corresponded to  $\pm 1.32\%$  strain, superimposed on the 10% prestrain. During testing, signals from a strain transducer (attached at one grip) and a

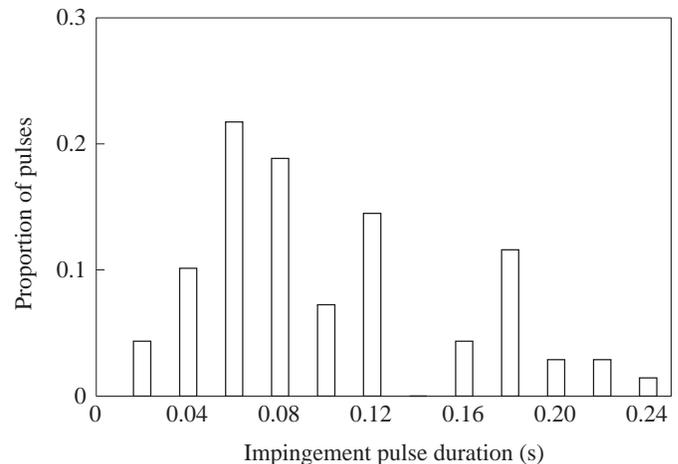


Fig. 2. Histogram of impingement force pulse duration from recordings conducted under approximately 70 breaking waves in the field.

force transducer (mounted at the other grip) were fed into a cross-channel spectrum analyzer (Wavetek model 5820A), allowing detection of the phase lag between stress and strain. At each frequency, the elastic and loss moduli were calculated from the spectral coefficients relating the in-phase and out-of-phase components of stress to strain. Ferry (Ferry, 1980) explains these relationships in detail. Since the mass density ( $\rho$ ) of most seaweeds is quite similar to that of sea water (Gaylord and Denny, 1997), it was assumed to equal  $1025 \text{ kg m}^{-3}$  for the purposes of the numerical experiments reported below.

Both the elastic modulus and the loss modulus of the two example species examined in this study, *Pelvetia compressa* and *Calliarthron cheilosporiodes* (for morphological descriptions, see Abbott and Hollenberg, 1976), varied little across a wide range of frequency (Fig. 3A,B). The elastic moduli shown in Fig. 3A are also of the same general magnitude as values reported previously for a variety of macroalgae ( $10^6$  to  $10^8 \text{ N m}^{-2}$ ; for a review, see Denny et al., 1989). Note that the small blips in the curves of Fig. 3A occurred in association with the natural modes of vibration of the experimental apparatus and do not represent actual discontinuities in the way that the elastic modulus varies with frequency.

#### *Tensile organisms*

We begin our exploration of the consequences of transient forces applied to organisms with differing structural attributes by examining the simplified case of an idealized plant or animal that resists forces primarily in tension, as do many floppy seaweeds once they have passively reoriented to align with flow. Because we are concerned with the imposition of very brief loads, where stresses within an organism may not have time to reach equilibrium with the applied force, classical engineering expressions become invalid, and we must consider the propagation of stress waves through the organism. In such

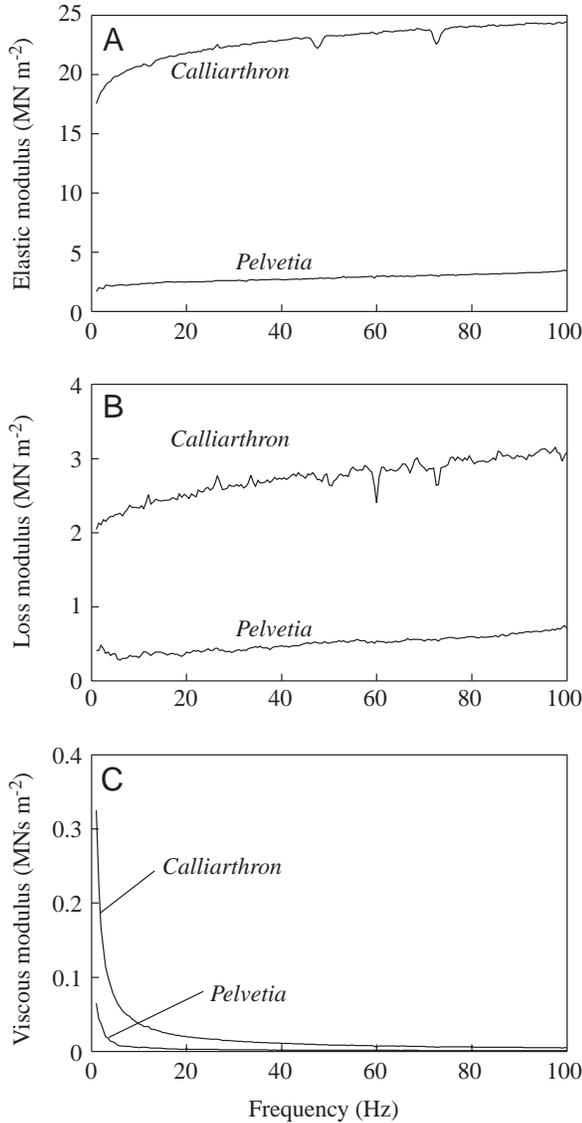


Fig. 3. Material properties of two example species of seaweed, a coralline red alga, *Calliarthron cheilosporiodes*, and a brown rockweed, *Pelvetia compressa*. Measurements on *C. cheilosporiodes* used the genicula, the compliant regions connecting its calcium carbonate nodules (see Abbott and Hollenberg, 1976). (A) Elastic moduli,  $E$ . (B) Loss moduli,  $E_{\text{loss}}$ . (C) Viscous moduli,  $E_{\text{visc}}$ .

situations, the response of a thin, rod-like, viscoelastic organism subjected to an axial force  $F$  applied at its distal end (Fig. 4A) is governed by the longitudinal wave equation (Kolsky, 1963; see Appendix):

$$\rho \frac{\partial^2 \xi}{\partial t^2} = E \frac{\partial^2 \xi}{\partial x^2} + E_{\text{visc}} \frac{\partial^3 \xi}{\partial t \partial x^2}, \quad (4)$$

where  $\xi$  is the axial displacement of the tissues at a given position ( $x$ ) and time ( $t$ ) within the organism.  $E_{\text{visc}}$  is the viscous modulus, a material parameter that can be calculated as  $E_{\text{loss}}/\omega$  from the experimental measurements, where  $\omega$  is the frequency of loading in  $\text{rad s}^{-1}$ . Values of  $E_{\text{visc}}$  for *Calliarthron*

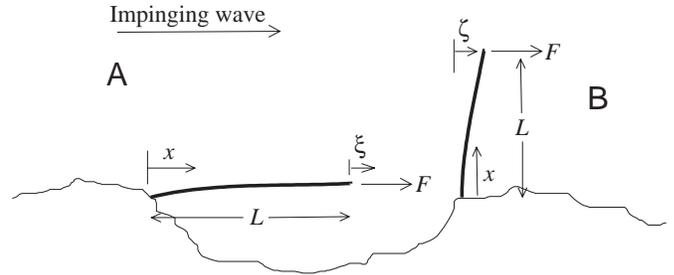


Fig. 4. The two simplified types of organism considered in this study. (A) Tensile organisms. (B) Organisms that bear applied loads primarily in bending.  $F$ , applied force;  $\xi$ , axial displacement of the organism's tissues at a given position  $x$ ;  $L$ , length of the organism;  $\zeta$ , lateral displacement at a given position  $x$ .

*cheilosporiodes* and *Pelvetia compressa* are shown in Fig. 3C. Equation 4 (termed a Voigt representation; Ferry, 1980) is a standard first-order model that accounts for both viscous and elastic characteristics. Boundary conditions are given in Table 1, where  $F$  is the applied force,  $A$  is the organism's cross-sectional area cut perpendicular to its long axis, and  $L$  is its length. We solve equation 4 numerically using standard finite difference techniques and a variation of the implicit Crank Nicolson method (see, for example, Ferziger, 1981).

For our first example, we present the response of a 10 cm long, relatively stiff, rod-like organism (length to diameter ratio 50) that has material properties similar to that of coral ( $E=5 \times 10^{10} \text{ N m}^{-2}$ ,  $\rho=2820 \text{ kg m}^{-3}$ ; Vincent, 1982; Lide, 1998) subjected to a 0.05 s duration, tensile pulse oriented parallel to its long axis. We begin by ignoring all damping, setting  $E_{\text{visc}}$  to zero, returning to a discussion of the effects of viscosity below. The pulse is assumed to exhibit the shape of the first half of a sine wave, as shown by the dashed line in Fig. 1B, which mimics the character of actual pulses recorded in the field.

In this first case, there are no surprises. The displacements induced at a given location within the organism vary in direct proportion to the instantaneous magnitude of the applied force. Displacements also increase with distance from the organism's point of attachment because of the additive effects of displacements of more proximal tissue elements (Fig. 5A). Similarly, the strains ( $\partial \xi / \partial x$ , which represent the localized degree of stretch) also vary in direct proportion to the instantaneous magnitude of the applied load, although they are constant throughout the organism (Fig. 5B). For generality, both the displacements and the strains in Fig. 5 are normalized by the maximal displacements or strains that would arise in response to a constant (i.e. static) force with the same magnitude as the peak of the applied pulse. This allows the consequences of any interactions between flexibility and the transient character of the load to be easily evaluated. When maximal normalized values differ from 1, this indicates important deviations from the effects of a static load. In this particular case, we find that the details of the propagation of stress waves are unimportant and that deformations remain

Table 1. Boundary conditions used with equations 4 and 5 in the numerical experiments

	Basal end ( $x=0$ )	Distal end ( $x=L$ )
Tensile organisms	$\xi(0,t)=0$	$F(t) = EA \frac{\partial \xi}{\partial x}(L,t) + E_{\text{visc}} A \frac{\partial^2 \xi}{\partial t \partial x}(L,t)$
Organisms in bending	$\zeta(0,t)=0$	$-EI \frac{\partial^2 \zeta}{\partial x^2}(L,t) - E_{\text{visc}} I \frac{\partial^3 \zeta}{\partial t \partial x^2}(L,t) = 0$
	$\frac{\partial \zeta}{\partial x}(0,t) = 0$	$F(t) = -EI \frac{\partial^3 \zeta}{\partial x^3}(L,t) - E_{\text{visc}} I \frac{\partial^4 \zeta}{\partial t \partial x^3}(L,t)$

All symbols are defined in the list of symbols.

essentially in equilibrium with the external force throughout the time course of its application. In other words, the ultimate effects of the brief force pulse are exactly what we would expect if we simply noted its magnitude alone.

Consider, however, a longer ( $L=1$  m, again with a length to diameter ratio of 50) and compliant, undamped, rod-like organism with elastic material properties akin to those reported above for seaweeds ( $E=10^7$  N m<sup>-2</sup>,  $\rho=1025$  kg m<sup>-3</sup>). When this flexible organism is subjected to a 0.05 s half-sine tensile force

pulse, we observe a very different outcome from that for the short, stiff organism. Maximum displacements now overshoot static values by 50% (Fig. 6A). We also observe oscillations continuing after cessation of the force pulse. These oscillations represent vibration at the organism's natural frequency. Although analogous oscillations do, in fact, occur within the organism of Fig. 5 as well, they are of imperceptibly small amplitude since the pulse applied to the short, stiff organism

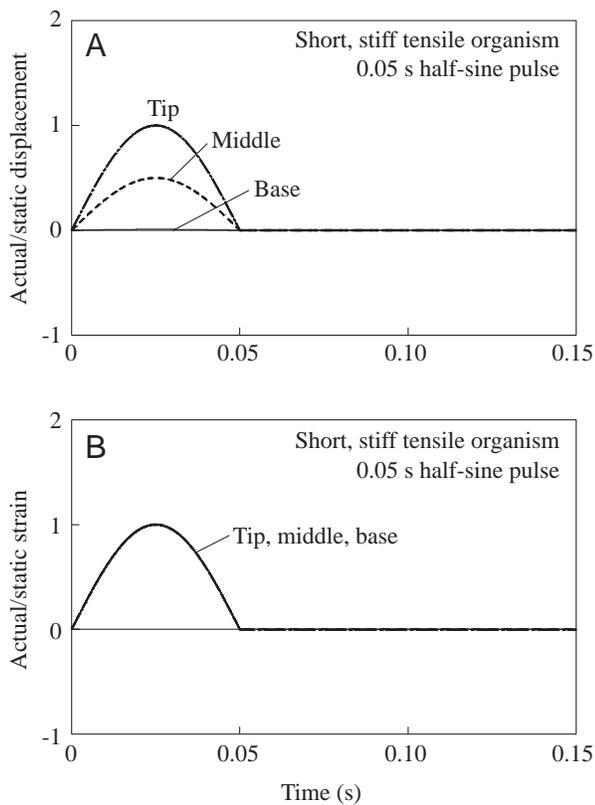


Fig. 5. Response of a short and stiff organism to a 0.05 s half-sine tensile force pulse.  $L=0.1$  m,  $E=5 \times 10^{10}$  N m<sup>-2</sup>,  $\rho=2820$  kg m<sup>-3</sup>. (A) Observed axial displacements at three locations along the length of the organism, relative to the displacement that would arise at the tip of the organism if the load were constant. (B) Observed strains relative to the strain that would arise if the load were constant.  $L$ , length;  $E$ , elastic modulus;  $\rho$ , mass density.

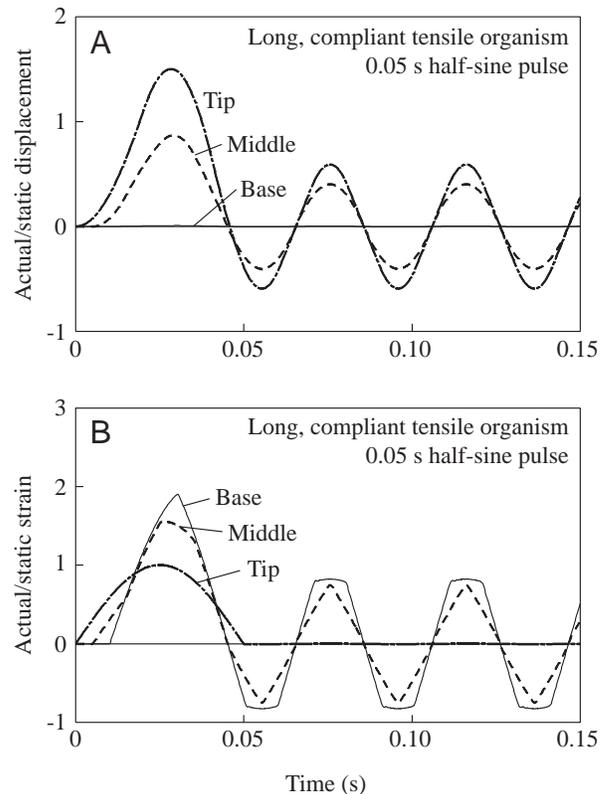


Fig. 6. Response of a long and compliant organism to a 0.05 s half-sine tensile force pulse.  $L=1$  m,  $E=10^7$  N m<sup>-2</sup>,  $\rho=1025$  kg m<sup>-3</sup>. (A) Observed axial displacements at three locations along the length of the organism, relative to the displacement that would arise at the tip of the organism if the load were constant. (B) Observed strains at three locations within the organism, relative to the strain that would arise if the load were constant.  $L$ , length;  $E$ , elastic modulus;  $\rho$ , mass density.

varies over time scales that are much longer than the organism's natural period, imparting little energy at its resonant frequency. We also note differences between Figs 5B and 6B in the character of the strains induced in the organisms. In the case of the longer, compliant organism, we find that the strains developed in its tissues are no longer uniform along its length, but now vary strongly with position (Fig. 6B). Maximal strains occur at the base of the organism where it attaches to the substratum, with magnitudes approaching values twice as large as those arising from a constant force. As discussed further below, this doubling of strain is tied to the fact that the rise time of the force pulse is short relative to the time it takes a stress wave to propagate the length of the organism. In this particular situation, therefore, we find that being longer and more compliant actually exacerbates the consequences of the brief load in question. This conclusion is exactly the opposite of what one would expect given traditional qualitative remarks regarding the operation of flexible, biological 'shock absorbers'.

*Organisms in bending*

Of course, not all intertidal plants and animals necessarily bear loads in tension. Many have erect growth forms and are subjected predominantly to lateral forces that tend to bend them. As we shall see, the consequences of brief loads of given duration under such lateral loading conditions can differ dramatically from their tensile analogues.

The propagation of waves of bending in a viscoelastic, rodlike organism subjected to a lateral force applied at its distal tip (Fig. 4B) is given by (Graff, 1975; see Appendix):

$$\rho A \frac{\partial^2 \zeta}{\partial t^2} = -EI \frac{\partial^4 \zeta}{\partial x^4} - E_{\text{visc}} I \frac{\partial^5 \zeta}{\partial t \partial x^4}, \quad (5)$$

where  $\zeta$  is the displacement perpendicular to the undeformed long axis of the organism at a particular location ( $x$ ) and time ( $t$ ) within the organism and  $I$  is the second moment of area of the organism cross section (here  $\pi r^4/4$ , where  $r$  is the cross section radius; see, for example, Denny, 1988), cut perpendicular to the organism's long axis. The product  $EI$  is the flexural stiffness, an index of the plant or animal's resistance to bending. The boundary conditions for equation 5 are given in Table 1.

Considering once again an undamped, short and stiff coral-like organism subjected to a 0.05 s half-sine force pulse, this time applied laterally as in Fig. 4B, we see a very different behavior from the tensile loading scenario. Unlike in the tensile case (Fig. 5), the normalized displacements do not track the force trajectory smoothly, but instead oscillate about the underlying sinusoidal curve (Fig. 7A). The longitudinal strains within the organism (calculated as  $r\partial^2\zeta/\partial x^2$ ; Gere and Timoshenko, 1990) also vary as a function of location (Fig. 7B), much as they did in the flexible, longer tensile organism of Fig. 6B. Fig. 8 plots multiple snapshots of the entire organism oscillating to illustrate more clearly the nature of the bending motion. Note, however, that in spite of the

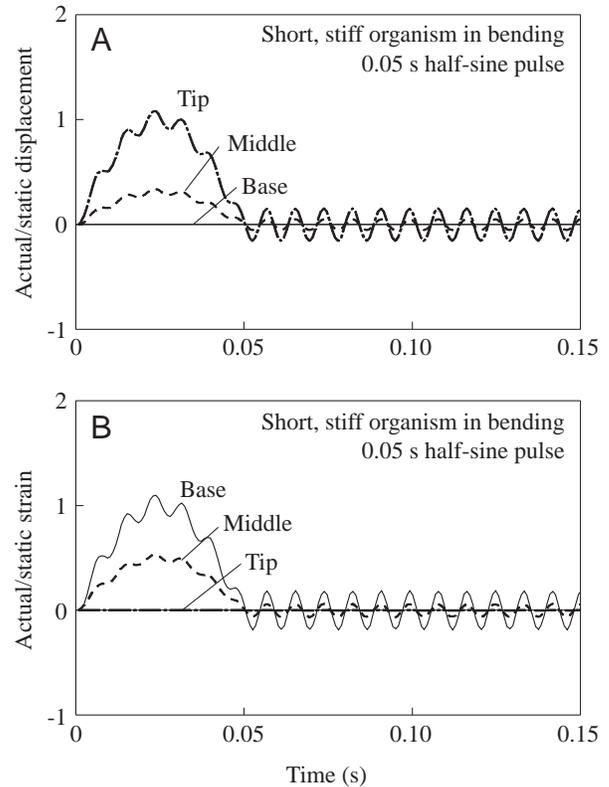


Fig. 7. Response of a short and stiff organism to a 0.05 s half-sine lateral force pulse.  $L=0.1\text{ m}$ ,  $E=5\times 10^{10}\text{ N m}^{-2}$ ,  $\rho=2820\text{ kg m}^{-3}$ . (A) Observed lateral displacements at three locations along the length of the organism, relative to the displacement that would arise at the tip of the organism if the load were constant. (B) Observed strains relative to the maximum strain that would arise at the base of the organism if the load were constant.  $L$ , length;  $E$ , elastic modulus;  $\rho$ , mass density.

spatio-temporal variation shown in Figs 7 and 8, the peak normalized displacements and strains do not differ markedly from 1.

This final point does not hold true in the case of the longer, compliant, undamped organism subjected to a 0.05 s lateral half-sine force pulse. In this case, displacements and strains do not resemble the force trajectory in the slightest (Fig. 9). Indeed, their magnitudes during the first 0.15 s following imposition of the force (the standard time window used in Figs 5–7) are miniscule. It is only when we expand our observations to longer times that oscillations become apparent (Fig. 10). In the case of displacements, the primary motions occur with a period of approximately 3 s, with higher-frequency components superimposed (Fig. 10A). The strain trajectories are even more complicated because of the reflection and superposition of multiple modes of bending (Fig. 10B). Even after 7.5 s, no clear repeatable pattern is discernible. Although higher-order fluctuations would, of course, damp out in any true material with finite viscosity, the complexity of the displacement and strain time series is still striking (for snapshots showing the nature of the oscillations of the entire organism, see also

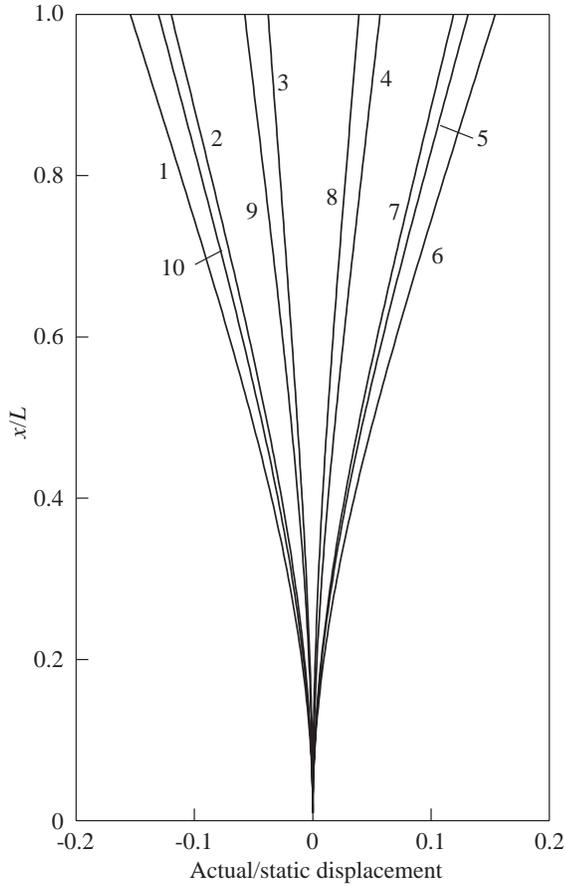


Fig. 8. Pattern of lateral oscillations occurring in Fig. 7 after cessation of the force pulse. Ten snapshots of displacement as a function of position  $x$  along the length  $L$  of the organism are shown, evenly spaced through one oscillatory period. The displacements are normalized by the displacement that would be produced at the tip of the organism by a constant force.

Fig. 11). The most important point of Fig. 10, however, is the fact that the peak magnitudes of both the displacements and the strains are far smaller than one would expect simply on the basis of the magnitude of the applied force (less than 30% as large in the case of the strains). This situation therefore provides a classic example of a situation in which the consequences of a brief load are greatly attenuated by organism inertia.

*The fundamental governing parameters*

The differences among the dynamic behaviors observed in Figs 5–11 illustrate the need for a better understanding of the interactions between organisms and transient loads. In addition, real plants and animals are not perfectly elastic but possess viscous traits as well. As it turns out, by nondimensionalizing equations 4 and 5, we can specify completely, using only two underlying dimensionless parameters, the maximal normalized strains produced by force pulses in viscoelastic organisms of the simplified form we model here.

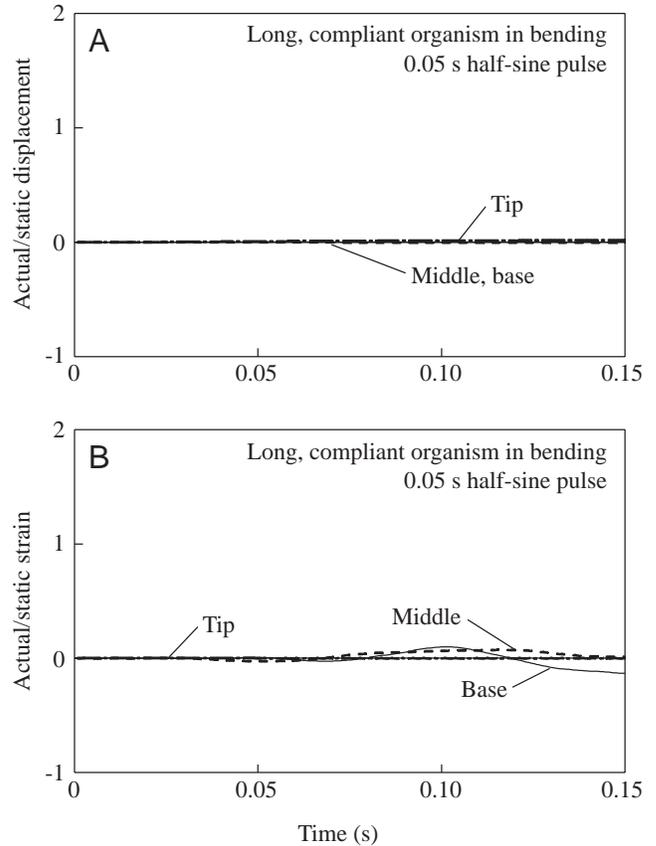


Fig. 9. Response of a long and compliant organism to a 0.05 s half-sine lateral force pulse, during the first 0.15 s following imposition of the force.  $L=1$  m,  $E=10^7$  N m<sup>-2</sup>,  $\rho=1025$  kg m<sup>-3</sup>. (A) Observed lateral displacements at three locations along the length of the organism, relative to the displacement that would arise at the tip of the organism if the load were constant. (B) Observed strains relative to the maximum strain that would arise at the base of the organism if the load were constant.  $L$ , length;  $E$ , elastic modulus;  $\rho$ , mass density.

In the case of tensile organisms, the two fundamental parameters are:

$$\tau_{\text{tension}} = \frac{T \sqrt{E/\rho}}{4L}, \tag{6}$$

$$\eta_{\text{tension}} = \frac{E_{\text{visc}} \sqrt{E/\rho}}{4EL}. \tag{7}$$

$\tau_{\text{tension}}$  represents the pulse period,  $T$  (which is twice the pulse duration since the force lasts for only half a full sine wave), relative to the natural period of longitudinal vibration of the organism [ $4L/\sqrt{(E/\rho)}$ ; see Graff, 1975]. It is therefore a nondimensional form of the pulse period.  $\eta_{\text{tension}}$  represents the retardation time ( $E_{\text{visc}}/E$ ; Ferry, 1980) of the material from which the organism is constructed relative to the organism's natural period of longitudinal vibration. The retardation time quantifies how slowly a material responds to a sudden change in force, a measure of how viscously it behaves. Thus,  $\eta_{\text{tension}}$

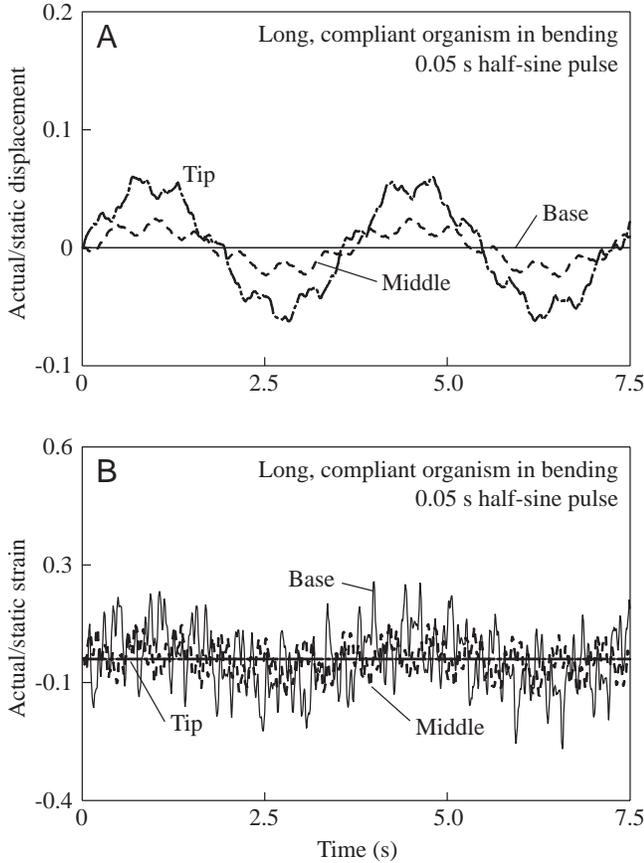


Fig. 10. Response of the organism of Fig. 9 extended to longer times.

is an index of nondimensional damping. Fig. 12A shows the relationship between these parameters and the peak normalized strains produced by half-sine tensile pulses of a range of periods.

In the case of organisms in bending, the two governing parameters are analogous:

$$\tau_{\text{bending}} = 0.56 \frac{T}{L^2} \sqrt{\frac{EI}{\rho A}}, \quad (8)$$

$$\eta_{\text{bending}} = 0.56 \frac{E_{\text{visc}}}{EL^2} \sqrt{\frac{EI}{\rho A}}. \quad (9)$$

$\tau_{\text{bending}}$  represents the pulse period divided by the natural period of the primary mode of bending oscillation [ $1.79L^2/\sqrt{(EI/\rho A)}$ ; see Graff, 1975], and  $\eta_{\text{bending}}$  equals the retardation time divided by the natural period of the primary mode. Fig. 12B shows the relationship between these parameters and the peak normalized strains produced by half-sine lateral pulses of a range of periods.

There are a number of similarities as well as a number of important differences between Fig. 12A and 12B. For instance, both tensile organisms (Fig. 12A) and organisms in bending (Fig. 12B) can experience strains either less than or greater than static strains, depending on the duration of the force pulse and the degree of damping. We have already observed a subset

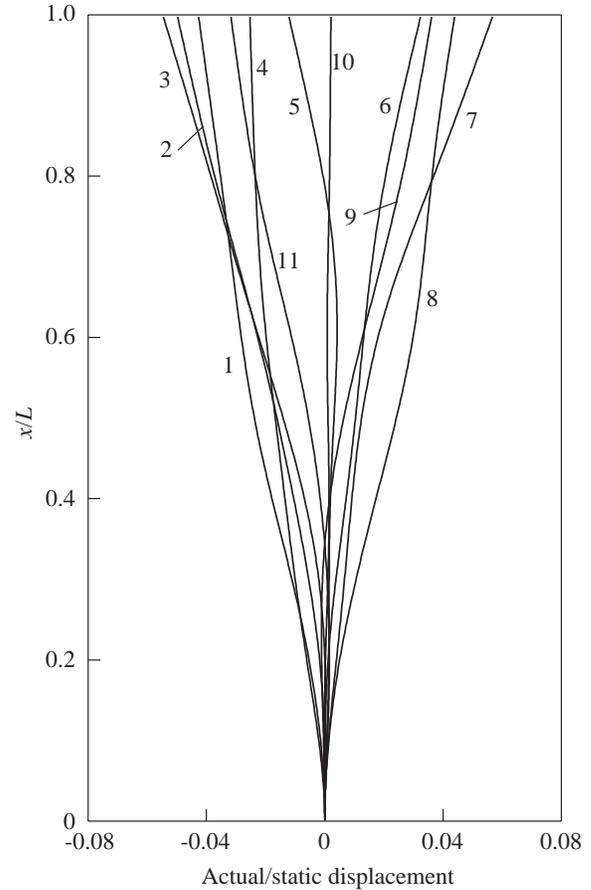


Fig. 11. Pattern of lateral oscillations occurring in Fig. 10 after cessation of the force pulse. Eleven snapshots of displacement as a function of position  $x$  along the length  $L$  of the organism are shown, evenly spaced through approximately one oscillatory period. The displacements are normalized by the displacement that would be produced at the tip of the organism by a constant force.

of these possibilities in Figs 5–11. In the case of tensile organisms of the simplified form we model here, however, there is an underlying tendency for force pulses that are short enough (i.e. far enough to the right in Fig. 12A) to produce maximal strains that are double those resulting from a constant force. Only the presence of viscous damping offsets this effect.

For organisms subjected to bending, in contrast, substantial decreases in force pulse duration result in an attenuation of maximal strain even in the absence of damping. Although peak strains can still exceed static values by a factor of as much as 2, this strain exacerbation occurs only in a narrow range in which there is tuning between the organism's natural period of oscillation and the pulse period. This situation is analogous to what happens in the initial stages of resonance in plants or animals that are forced periodically (as opposed to with a finite pulse) near their natural frequency (Denny et al., 1998). As  $\tau_{\text{bending}}$  decreases, the normalized maximal strains decline dramatically as a consequence of organism inertia, leading to the behavior seen previously in Fig. 10.

The general curves of Fig. 12 therefore serve to emphasize

two important points. First, an increase in response time (i.e. greater compliance) does not always lead to an amelioration of the consequences of a brief force. In fact, in the case of a relatively long pulse, where  $1/\tau_{\text{tension}}$  or  $1/\tau_{\text{bending}}$  is less than 1, an increase in response time can produce higher strains. Second, even when response times are much longer than the duration of an applied force (i.e. if  $1/\tau_{\text{tension}}$  or  $1/\tau_{\text{bending}}$  is much greater than 1), attenuation of the effects of that force occur consistently only in organisms that carry that load in bending and/or are substantially viscously damped. We note that the inertial attenuation that occurs in bending arises because a bending load lasting shorter than the time required for a stress wave to propagate the length of the organism cannot generate a contiguous lever arm all the way to the base of the organism, and axial strains vary roughly in proportion to that lever arm (we ignore the effects of shear; see, for example, Timoshenko, 1937). In contrast, strains in simple tensile organisms depend only on the local effects of a force (there is no lever arm).

Fig. 12 encompasses the total possible parameter space for the loading scenarios we consider. In practice, however, only

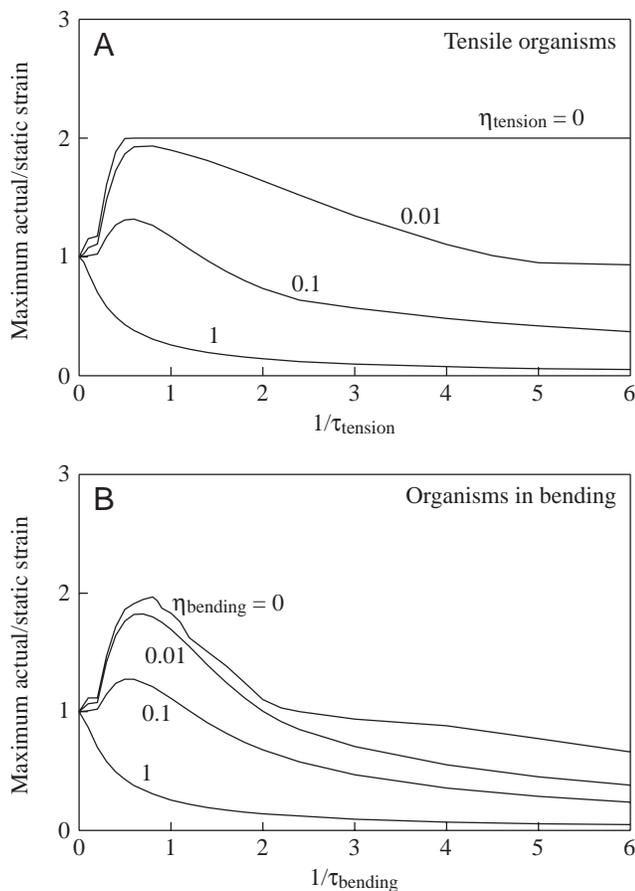


Fig. 12. Peak strains resulting from half-sine pulses, relative to the maximum strains that would arise in response to constant forces, as a function of nondimensional pulse duration ( $\tau_{\text{tension}}$  or  $\tau_{\text{bending}}$ ) and nondimensional damping ( $\eta_{\text{tension}}$  or  $\eta_{\text{bending}}$ ). (A) Tensile organisms. (B) Organisms in bending. Note the capacity for inertial attenuation in the bending case.

a subset of this overall space may be available to real plants and animals since particular species-specific characteristics (material properties, for example) may constrain the values of component parameters in equations 6–9. In the case of the algae we test in this study, ratios of nondimensional pulse period to nondimensional damping ( $\tau/\eta$ ) are essentially constant across frequency, with  $\tau$  roughly equal to  $50\eta$  in either tension or in bending, for both *Calliarthron cheilosporiodes* and *Pelvetia compressa* (Fig. 13A). Given this relationship, these algae will span only particular trajectories through Fig. 12A,B. As is shown in Fig. 13B, the course of these trajectories suggests that seaweeds may often be so lightly damped that they experience substantial attenuation of brief forces primarily only in bending. Table 2 lists, for reference, the nondimensional pulse periods corresponding to the cases examined in Figs 5–11.

#### Size and shape

Equations 6–9 and the data of Figs 12 and 13 include

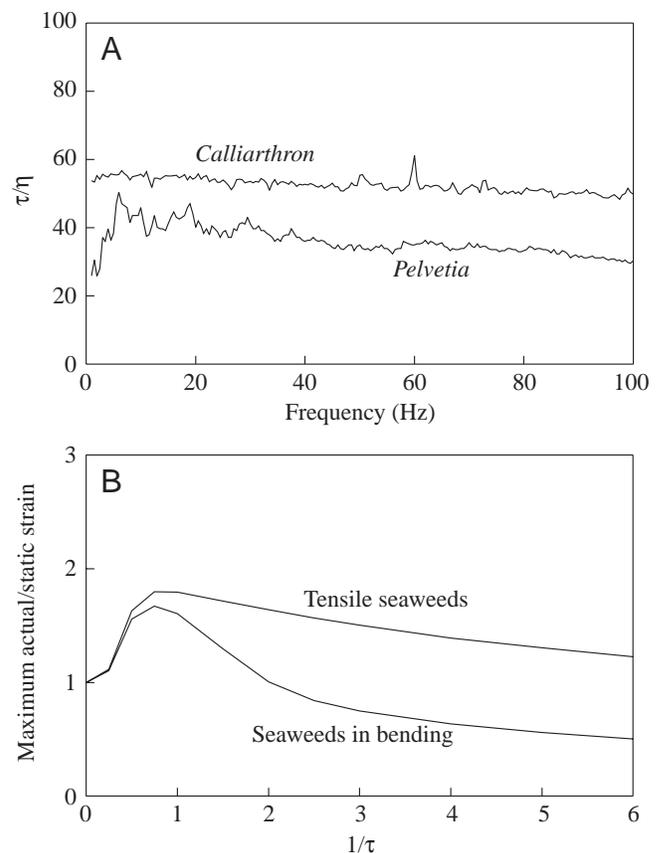


Fig. 13. Dynamic properties of macroalgae. (A) The ratio of nondimensional pulse period,  $\tau$ , to nondimensional damping,  $\eta$ . The subscripts of equations 6–9 have been dropped since this ratio is identical in tension and bending. (B) Peak macroalgal strains resulting from half-sine pulses, relative to the maximum strains that would arise in response to constant forces, as a function of nondimensional pulse duration. These curves correspond to the trajectories through Fig. 12A,B defined by  $\tau=50\eta$ .

Table 2. Dimensionless parameter values governing the maximal dimensionless strains induced by a 0.05 s half-sine force pulse in the model organisms of Figs 5–11

	Tension		Bending	
	$1/\tau_{\text{tension}}$	$\eta_{\text{tension}}$	$1/\tau_{\text{bending}}$	$\eta_{\text{bending}}$
Short and stiff coral	$9.5 \times 10^{-4}$	0	0.085	0
Long and compliant seaweed	0.41	0	36	0

$\tau_{\text{tension}}$ , nondimensional form of pulse period for an organism in tension;  $\tau_{\text{bending}}$ , nondimensional form of pulse period for an organism in bending;  $\eta_{\text{tension}}$ , index of nondimensional damping for an organism in tension;  $\eta_{\text{bending}}$ , index of nondimensional damping for an organism in bending.

intrinsically the effects of organism size. Although it is perhaps intuitive that longer organisms have longer response times (i.e. their natural periods of motion are greater relative to a particular pulse period, resulting in smaller values of  $\tau$ ), it is also true that increases in  $L$  lead to lower effective levels of viscous damping. A close examination of Fig. 12 reveals that such changes to  $\eta_{\text{tension}}$  or  $\eta_{\text{bending}}$  can affect the maximal strains as much as or more than the accompanying shift in the organism's natural period of motion. Changes in size are also likely to be relatively more important than equivalent percentage shifts in material stiffness, since  $E$  is raised only to the  $\pm 1/2$  power in the dimensionless parameters, while  $L$  appears linearly or is squared.

There are also differences in the way the dynamics of organisms subjected to tensile or bending pulses depend on shape. In equations 6 and 7, which govern simple tensile organisms, we find that the only parameter related to morphology is plant or animal length ( $A$  does not appear). In contrast, in equations 8 and 9, which govern organisms in bending, we find not only a greater sensitivity to  $L$  (it is squared), but two other composite shape-dependent terms appear as well:  $EI$  and  $\rho A$ . The first composite term, *via* its inclusion of  $I$ , accounts for the influence of the distribution of tissue about the axis of bending, a factor that has important implications for how effectively a plant or animal will resist a lateral load. The second composite term is the mass per unit length, a measure of how stocky the organism is. Together, the appearance of these two variables in the dimensionless parameters for bending indicate that shape plays a relatively critical role in setting peak strains for organisms loaded by brief lateral forces. Note, however, that if there are strong discontinuities in distributions of mass along the length of an organism loaded either in tension or in bending, these discontinuities can affect an organism's dynamics. Unfortunately, although such effects are likely to be important in many real plants and animals, a full analysis of their consequences awaits further study.

#### Reconfiguration, reorientation and 'going with the flow'

The numerical experiments we have conducted here have

assumed implicitly that the applied force is independent of the response of the organism to that force. This has greatly simplified the underlying analysis. However, in reality, exceptionally compliant organisms subjected to large hydrodynamic loads may deform sufficiently during the application of a force that the force itself changes. This occurs whenever deformations are severe enough to alter substantially the way the fluid flows relative to the plant or animal.

Generally, the alteration of relative flow acts to decrease the externally applied load. However, because an organism also acquires momentum while deforming, such behavior may also engender a susceptibility to subsequent inertial forces imposed as a moving plant or animal reaches the limit of its range of motion and gets 'jerked' to a halt by its tether. Mathematically, this effect derives from an increase in the  $d^2\xi/dt^2$  term in force balances of the form of equation 1. Denny et al. (Denny et al., 1997; Denny et al., 1998) and Gaylord and Denny (Gaylord and Denny, 1997) have explored this topic in some detail, noting that such inertial effects ensure that deformation (even with its reduction of applied external load) provides a net advantage only under certain circumstances.

Two of the more common situations in which deformation may alter applied forces to a net advantage have already been mentioned in the Introduction. One is the case of plants or animals that passively reconfigure (becoming more streamlined) in response to relatively slowly applied loads. In this scenario, an organism deforms, but the rates of deformation are so slow that the organism gains little momentum. This prevents a finite inertial force from being imposed. A second case in which deformation has been proposed to provide benefit arises for large kelps in subtidal habitats (Koehl, 1982; Koehl, 1984; Koehl, 1986). Although these organisms do acquire substantial momentum while swaying beneath waves, the bidirectional flows to which they are subjected often reverse before longer individuals reach the end of their tethers. This may allow individuals to gain the benefits of decreased relative fluid velocities without having to cope with the negative consequences of rapid deceleration. Further study of this topic is needed for conclusive verification, however.

Reorientation or 'going with the flow' behavior is less likely to be advantageous in intertidal regions. In the surf zone, where flows may travel tens of meters before reversing, even relatively long organisms routinely become fully extended. Under these conditions, being longer often just postpones the imposition of a force, rather than decreasing its magnitude. Of course, brief loads (such as those associated with the impingement of waves on emergent organisms on the shore; Fig. 1) often last shorter than the time required for reorienting tensile plants and animals to become extended in flow. Thus, many impingement forces may be expended largely in straightening compliant organisms rather than in producing dangerous deformations (for experimental evidence of this phenomenon, see Gaylord, 2000). However, in those somewhat rarer situations in which an organism is unlucky enough to be already extended when a wave arrives,

impingement forces may be applied essentially at full strength. Under these conditions, the length of the organism continues to play a role in determining response time, as described in Figs 12 and 13.

### Concluding remarks

Traditional views regarding the design of benthic marine organisms have emphasized three potential advantages of low stiffness and extensibility: (i) an enhanced ability to reconfigure or reorient in flow (resulting in improved streamlining or a reduction in relative flow speed), with consequent decreases in applied force, (ii) the ability to experience lower peak forces while absorbing equivalent amounts of energy, and (iii) a capacity for amelioration of the effects of brief loads *via* an increase in response time. Point i appears to provide robust benefits as long as the organism avoids the specter of excessive momentum. Unfortunately, although points ii and iii are appealing in their simplicity and may be relevant under a subset of conditions, they are also unlikely to be applicable in a fully general context.

In the case of point ii, emphasizing the advantages of extensibility-mediated energy absorption, there is an implicit assumption of a specific type of loading that is at odds with what is experienced by many plants and animals in flow. This incongruence leads to predictions that may be exactly the opposite of what happens in some circumstances in nature. For example, longer tensile organisms would be expected always to experience lower strains than shorter organisms with the same modulus and cross-sectional area since equivalent amounts of energy are more readily absorbed by greater volumes of tissue. As Figs 5 and 6 show, however, if it is the force that is dictated rather than the energy, as may be typical of many organisms in flow, then longer plants and animals that are subjected to the same potential static strain can at times actually experience greater realized strains than their shorter counterparts.

In the third point, which suggests that higher compliance increases response times and ameliorates the consequences of brief loads, we also find a need for qualification. In the case of organisms with strong discontinuities in shape, dynamic models can often be simplified by ‘lumping’ mass elements at specific localized regions (for valid applications of this approach, see, for example, Denny et al., 1998) since the relatively inefficient transmission of stress waves across discontinuities provides a propagation ‘bottleneck’ dominating the overall response of the organism. Under these conditions, attenuation of rapidly varying forces *via* increased response time may be a routine outcome. However, we notice that, when internal stress waves propagate within organisms of more uniform shapes, strains produced even by exceptionally brief loads need not be attenuated. Indeed, in the case of tensile organisms, it may be more typical for the effects of very brief loads to be doubled compared with static expectations. It is primarily in organisms that bear forces in bending in which opportunities for amelioration of brief forces occur. However, it is also clear that, even in organisms that bear

applied loads in bending, where inertial attenuation is a common component of the dynamics, increased compliance is not always beneficial. When increased flexibility causes the period of an applied pulse to correspond to the natural period of oscillation of an organism, internal strains are once again elevated. Viscous damping can offset such effects, but not all surf-zone organisms (seaweeds seem to be an example; Fig. 13B) appear to possess sufficient internal viscosity to take full advantage of such processes.

Clearly, there are other important factors that affect the basic issues explored in this study. In particular, most organisms do not exhibit constant stiffness (see, for example, Purslow, 1991; also see Gaylord and Denny, 1997 for analogous effects of large deflections in bending). Many plants and animals also have material properties that vary as a function of location within an organism (e.g. Koehl and Wainwright, 1977; Vincent and Gravell, 1986) or depend on whether the organism is stretched or compressed (e.g. Biedka et al., 1987; Gaylord and Denny, 1997). Perhaps most critically, many intertidal plants and animals possess complicated morphologies that resemble only marginally (or not at all) the simplified shapes we analyze here. Such complexities of shape can influence dramatically how stress waves propagate through an organism, as noted above. Furthermore, many forces are applied not as concentrated loads but are instead distributed across a finite region of an organism’s structure. Nevertheless, despite these additional (and important) complexities, the general patterns we describe here provide an initial framework for understanding a number of fundamental principles in the dynamics of benthic marine organisms. In particular, this study may be useful for evaluating the consequences of the brief and dangerous forces imposed by breaking waves as they impinge directly on emergent organisms on the shore.

## Appendix

### *Longitudinal viscoelastic waves*

The axial stress,  $\sigma$ , at a given location in a tensile organism is assumed to depend on both the axial strain and the rate of strain (see, for example, Kolsky, 1963):

$$\sigma = E \frac{\partial \xi}{\partial x} + E_{\text{visc}} \frac{\partial^2 \xi}{\partial t \partial x} . \quad (\text{A1})$$

A gradient in stress across an infinitesimal tissue element within the organism causes that element to accelerate according to Newton’s Second Law. Thus:

$$\frac{\partial \sigma}{\partial x} = \rho \frac{\partial^2 \xi}{\partial t^2} . \quad (\text{A2})$$

Substituting equation A1 into equation A2 yields equation 4 of the text.

### *Viscoelastic waves of bending*

Given the relationship of equation A1, the internal bending moment,  $M$ , at a given location in an organism in bending

depends both on the organism's curvature and on its rate of change of curvature (see, for example, Gere and Timoshenko, 1990):

$$M = -EI\kappa - E_{\text{visc}}I \frac{\partial \kappa}{\partial t}, \quad (\text{A3})$$

where  $\kappa$  is the curvature. For relatively small deflections:

$$\kappa = \frac{\partial^2 \zeta}{\partial x^2}. \quad (\text{A4})$$

Neglecting rotational effects, the transverse shear,  $V$ , is related to the internal moment by the standard expression of statics:

$$V = \frac{\partial M}{\partial x}. \quad (\text{A5})$$

Much as in equation A2, a gradient in shear across an infinitesimal tissue element causes that element to accelerate:

$$\frac{\partial V}{\partial x} = \rho A \frac{\partial^2 \zeta}{\partial t^2}. \quad (\text{A6})$$

Combining equations A3–A6 yields equation 5 of the text.

#### List of symbols

$A$	cross-sectional area
$E$	elastic modulus
$E_{\text{loss}}$	loss modulus
$E_{\text{visc}}$	viscous modulus
$F$	force
$F_{\text{external}}$	externally applied force
$F_{\text{max}}$	maximum force
$I$	second moment of area of the organism's cross section
$k$	stiffness
$L$	length
$m$	mass
$M$	internal bending moment
$r$	radius of a cross section
$t$	time
$T$	pulse period
$U$	velocity
$V$	transverse shear
$x$	given location within an organism
$\eta_{\text{bending}}$	index of nondimensional damping for an organism in bending
$\eta_{\text{tension}}$	index of nondimensional damping for an organism in tension
$\kappa$	curvature
$\rho$	mass density
$\sigma$	axial stress
$\tau_{\text{bending}}$	nondimensional form of pulse period for an organism in bending
$\tau_{\text{tension}}$	nondimensional form of pulse period for an organism in tension

$\omega$	frequency of loading
$\xi$	axial displacement
$\xi_{\text{max}}$	maximum extension
$\zeta$	lateral displacement

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