REVIEW PAPER

Ecological biomechanics of marine macrophytes

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Abstract

Macroalgae and seagrasses in coastal habitats are exposed to turbulent water currents and waves that deform them and can rip them off the substratum, but that also transport essential water-borne substances to them and disperse their propagules and wastes. Field studies of the physical environment, ecological interactions, and life history strategies of marine macrophytes reveal which aspects of their biomechanical performance are important to their success in different types of natural habitats and enable us to design ecologically relevant laboratory experiments to study biomechanical function. Morphology and tissue mechanical properties determine the hydrodynamic forces on macrophytes and their fate when exposed to those forces, but different mechanical designs can perform well in the same biophysical habitat. There is a trade-off between maximizing photosynthesis and minimizing breakage, and some macrophytes change their morphology in response to environmental cues. Water flow in marine habitats varies on a wide range of temporal and spatial scales, so diverse flow microhabitats can occur at the same site. Likewise, the size, shape, and tissue material properties of macrophytes change as they grow and age, so it is important to understand the different physical challenges met by macrophytes throughout their lives.

Keywords: Algae, biomechanics, ecomechanics, hydrodynamics, kelp, life history, marine macrophyte, plasticity, safety factor, seagrass.

Introduction

Biomechanics is the study of the physics of how biological structure determines how organisms perform mechanical functions such as moving and producing or resisting forces. Research at the interface between biomechanics and ecology ('ecological mechanics', Wainwright *et al.*, 1976; 'ecological biomechanics', Koehl, 1999; 'ecomechanics', Denny, 2012; Higham *et al.*, 2021; 'mechanical ecology', Bauer *et al.*, 2020) has enhanced our understanding of the function of both organisms and ecosystems. It has long been recognized that processes at the organismal level can determine the behavior of populations, communities, and ecosystems (Schoener, 1986; May *et al.*, 1989), and biomechanics is used as a tool to address ecological questions in a mechanistic way (reviewed by Koehl, 1989, 1996; Jumars, 1993; Denny and Wethey, 2001; Denny and Gaylord, 2010; Baskett, 2012; Denny, 2016). Ecological biomechanics is also used to identify how functional traits of organisms and physical constraints on their performance in variable environments can affect evolution (Wainwright and Reilly, 1994; Koehl, 1996; Kempes *et al.*, 2019; Higham *et al.*, 2021). Not only

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Abbreviations: ESF, environmental stress factor; PAR, photosynthetically active radiation.

can biomechanical studies help us address ecological and evolutionary questions, but conversely ecological studies can enhance or change our understanding of organismal–level biomechanical function. This review on the ecomechanics of bottom-dwelling ('benthic') marine macrophytes focuses on examples of how we can gain biomechanical insights if we couple field studies of the physical habitats, ecological roles, and life history strategies of organisms with our laboratory analyses of their fluid dynamics and mechanical function. The purpose of this review of physical challenges faced by benthic marine plants and macroalgae and the features that affect their biomechanical performance in natural habitats is to complement the contributions in this special issue about the mechanical ecology of terrestrial plants.

Macroalgae (Fig. 1) and seagrasses (Fig. 2) are important components of marine ecosystems. The community and eco-system ecology of kelp forests (Stenneck *et al.*, 2002; Schiel and Foster, 2015), intertidal algal beds (Paine, 2002, 2010; Trowbridge *et al.*, 2010), and seagrass meadows (Larkum *et al.*, 2006; Orth, 2006; Hemminga and Duarte, 2008) have been studied extensively. Marine macrophytes provide food and habitat to a diversity of other organisms (Abbott and Hollenberg, 1976; Stenneck *et al.*, 2002; Graham, 2004; Graham *et al.*, 2007; Christie *et al.*, 2009). In addition, by intercepting light, altering ambient water flow, affecting sedi-mentation, and scouring the substratum, marine macrophytes determine the structure of benthic communities that develop under their canopies (e.g. Kennelly, 1989; Arkema *et al.*, 2009; Hughes, 2010). Marine macrophytes also provide ecosystem services such as protecting shorelines by damping waves and currents.

The physical environment of a marine macrophyte de-pends in part on the depth of the water. Water absorbs light, with longer wavelengths absorbed first, so the amount of photosynthetically active radiation (PAR) attenuates with depth. The 'euphotic zone' where enough light pene-trates for photosynthesis is confined to the upper ~200 m of the ocean, depending on water turbidity (Webb, 2017).
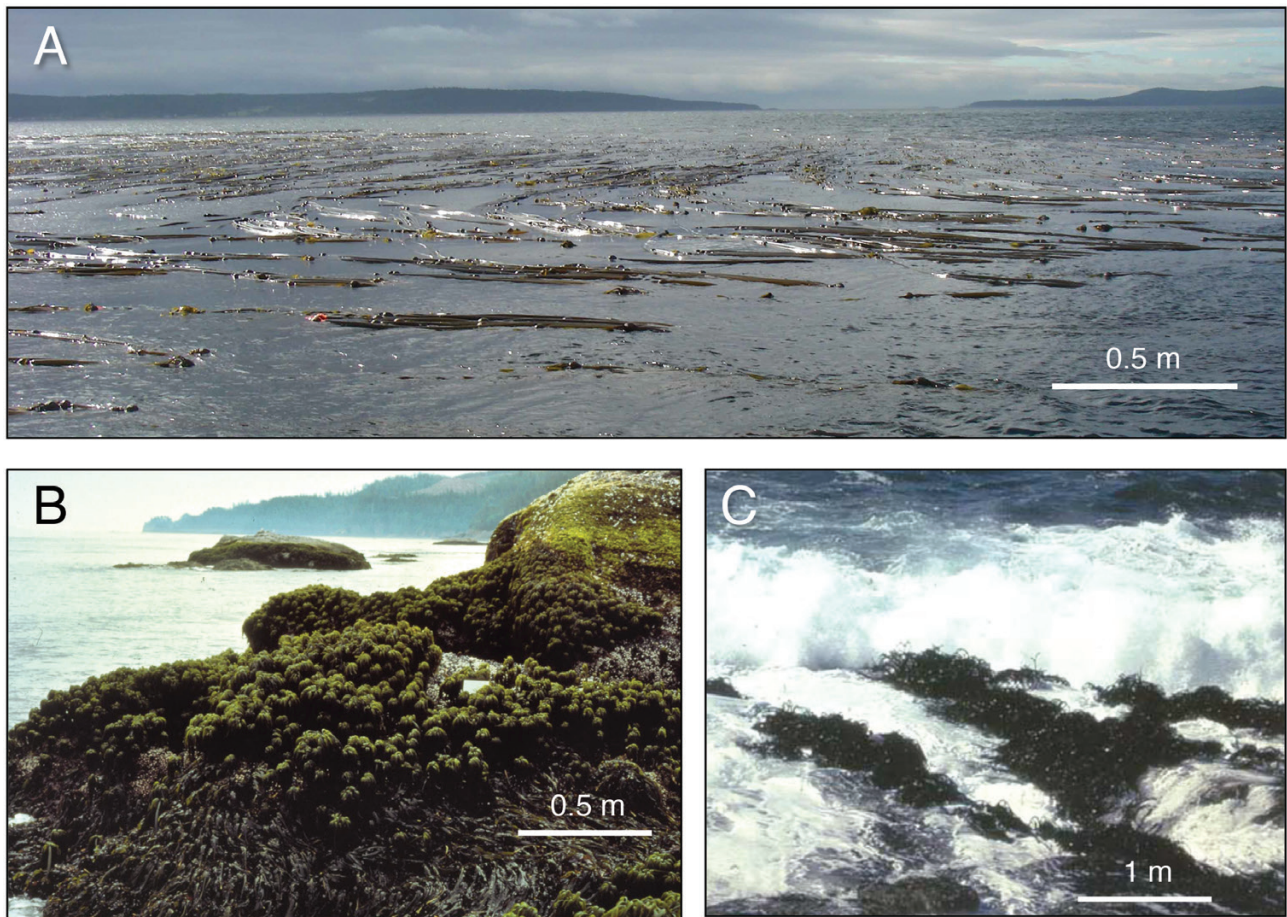
Fig. 1. Examples of macroalgae. (A) 'Giant bull kelp', *Nereocystis luetkeana*, growing in a tidal channel near San Juan Island, WA, USA. (B) Rocky shore seaweeds (including the upright 'sea palm', *Postelsia palmaeformis*, the long blade-like kelp *Alaria marginata* and *Hedophylum sessile,* and diverse bushy turf-forming algae) at low tide on Tatoosh Island, WA, USA. (C) Waves breaking on the intertidal kelp, *Lessonia nigrescens,* at high tide on a rocky shore, Valpariso, Chile (photographs by M. Koehl).
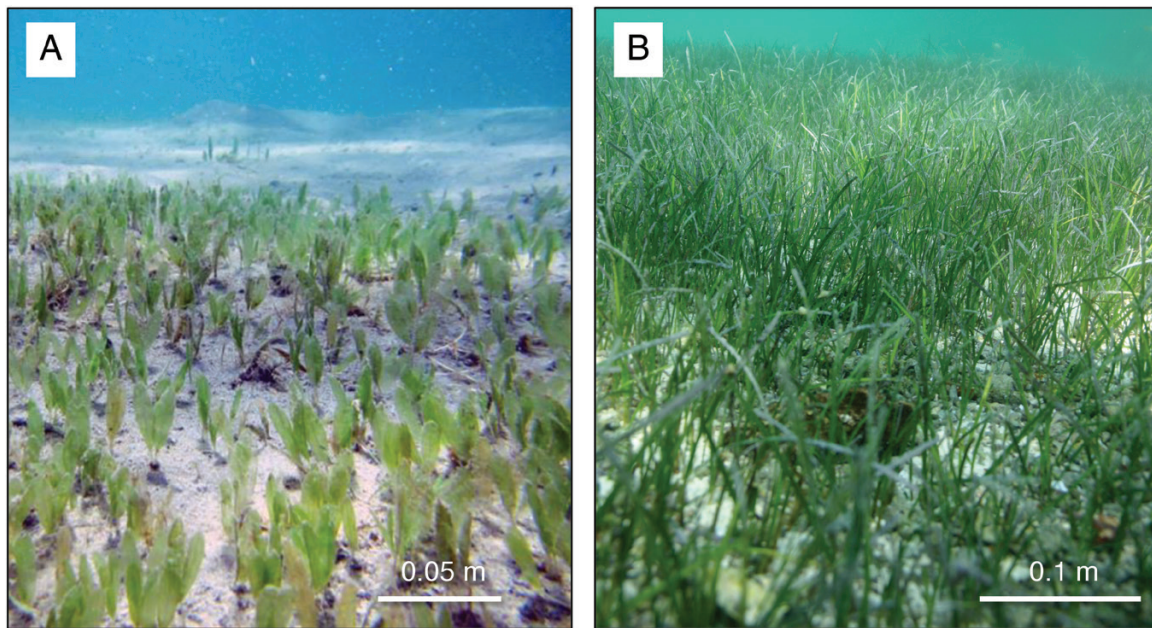
Fig. 2. Examples of seagrass meadows. (A) 'Paddle grass', *Halophila decipiens*, growing in a sandy habitat in Florida. (B) 'Eelgrass', *Zostera marina*, growing on a mud flat in North Carolina (photographs by Mark Fonseca).

Therefore, benthic macrophytes are confined to shallow regions of the ocean where they are exposed to turbulent currents and waves.

Macrophytes at the shallowest depths are often exposed to air when the tide goes out. Intertidal macrophytes must contend with desiccation and heating or freezing when exposed to air (Koehl and Wertheim, 2006). The fine-scale temporal and spatial distribution of these environmental challenges in intertidal habitats, the biophysics of heat and water exchange by intertidal organisms, and their physiological responses to such challenges is an area of active research (Helmuth *et al.*, 2010; Denny, 2016). Here I focus instead on the biomechanics of macrophytes in their hydrodynamic environments.

Because marine macrophytes are buoyed up by the surrounding water, gravity is not as important in constraining their biomechanical design as it is for terrestrial plants. Instead, water motion affects a variety of critical functions of macroalgae and seagrasses. Macrophytes attached to the substratum can be pushed over by moving water (thereby affecting light gathering) and they risk being broken or dislodged by ambient currents and waves, yet they also depend on that moving water for transport of dissolved nutrients and gases, removal of wastes and sediment, and dispersal of gametes and spores (reviewed in Norton *et al.*, 1981; Koehl, 1982, 1984, 1986, 1999; Denny, 1988; Vogel, 1994; Hurd, 2000; Koch *et al.*, 2006). Macroalgae have no roots, so they rely on uptake across thallus surfaces from the surrounding water for their supply of nutrients, carbon dioxide, and bicarbonate for photosynthesis, and other essential substances (Hurd, 2000). Although seagrasses have roots, they also take up dissolved resources through their leaves (Koch *et al.*, 2006; Stapel *et al.*, 2006; Nayar *et al.*, 2018).

Body designs that enhance a macrophyte's interaction with the water flowing around it improve transport, but also increase the hydrodynamic forces that can deform it or rip it off the subtratum.

Water flow in the habitats of marine macrophytes

Habitats in coastal marine regions are exposed to turbulent waves and water currents (Denny, 1988; Koehl and Wertheim, 2006; Simpson and Sharples, 2012) that are affected by the orientation and bathymetry of the shore, water depth, and local topography of a site (Denny, 1995; Helmuth and Denny, 2003; Gaylord *et al.*, 2007; O'Donnell and Denny, 2008). Benthic macrophytes in shallow coastal habitats are often exposed to waves (Fig. 3). At sites in which water depth is less than half of the crest to crest distance between waves, macrophytes on the sea floor are subjected to back and forth water flow with a period of seconds when a wave passes overhead, while blades on kelp up near the water surface encounter orbital water motion. Macrophytes attached to intertidal surfaces are exposed to breaking waves and to the rapid, turbulent shoreward flow and seaward backwash of broken waves (Fig. 4). Peak instantaneous water velocities and accelerations in breaking waves at intertidal sites are much higher than those under waves in deeper subtidal areas (Koehl, 1977, 1982, 1984; Denny, 1988; Denny *et al.*, 1985; Bell and Denny, 1994; Gaylord, 1999). However, net horizontal transport of water and water-borne materials across wavy shores is slow as the water sloshes back and forth (Koehl *et al.*, 1993; Koehl and Powell, 1994). While many
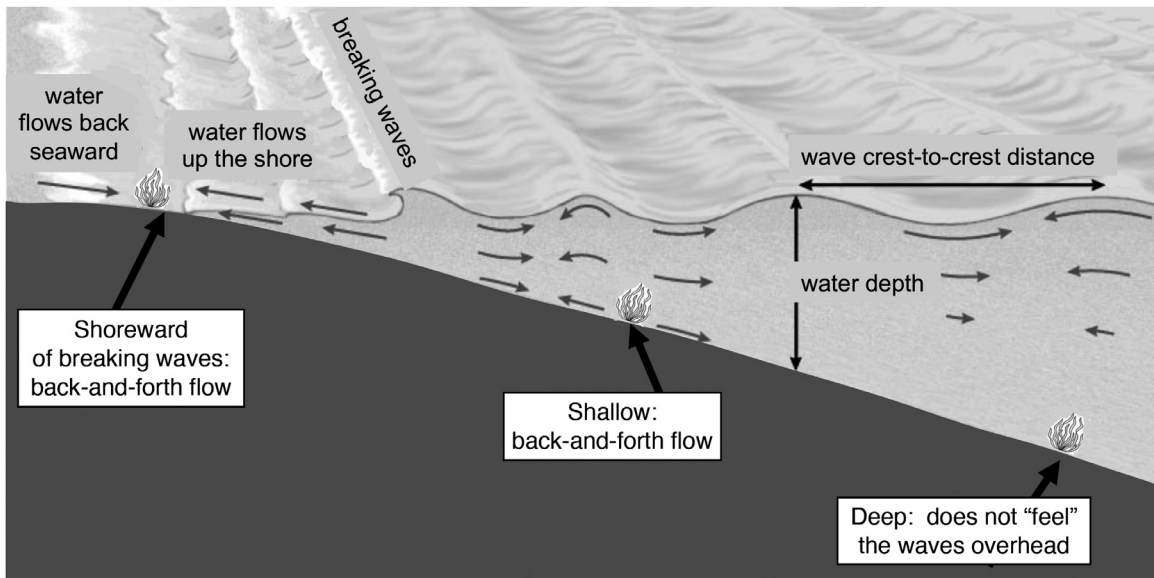
Fig. 3. Diagram of the water motion due to waves as they approach the shore. The water flow direction is indicated by the fine arrows in the water, and the substratum is shown in dark gray. Water flows shoreward under wave crests and seaward under wave troughs, so as a wave shape moves shoreward the water under it moves in a vertical orbit. The water motion associated with waves attenuates with depth, so a macrophyte growing in deep water does not 'feel' the waves passing overhead. However, if the depth is less than half the crest to crest distance between waves, then algae or seagrass on the sea floor experience back and forth flow due to waves. In the surf zone, macrophytes are exposed to breaking waves (Fig. 1C). Shoreward of breaking waves, macrophytes experience back and forth flow as water from broken waves rushes up the shore and then washes back seaward.

marine macrophytes encounter waves, others are exposed to unidirectional water motion. Macrophytes living in deep water that do not experience the back and forth flow of waves can encounter unidirectional currents, while those in tidal channels are subjected to water that flows in one direction for several hours and then in the opposite direction for several hours. These currents are turbulent, so instantaneous water velocities fluctuate (Koehl, 1984, 2000) and materials transported by the flowing water are spread by swirling eddies (Hurd, 2000).

The water flow encountered by a marine macrophyte at a particular site depends on its size and on the abiotic and biotic topography of its neighborhood (Koehl, 1977, 1982, 1984, 1986; O'Donnell and Denny, 2008). Water flow close to the substratum is much slower than flow farther from the bottom (reviewed in Koehl, 1984; Nowell and Jumars, 1984; Denny, 1988; Vogel, 1994; Koehl, 1999) (Fig. 4), so tall and short organisms side by side on the same rock (Fig. 1B) can be in different flow microhabitats. Therefore, it is important to measure flow in the field on the spatial scale encountered by the organism being studied. The water motion macrophytes experience also varies with time on scales from fractions of a second in waves and turbulence, to hours and days as the tides and weather change, and to seasons and years when periods of heavy wave action are more or less frequent (Sousa, 1979; Paine and Levin, 1981; Denny, 1988, 1995; Koehl, 1999; Wolcott, 2007; Burnett and Koehl, 2019). Technical approaches to measure water flow in the field on the spatial and temporal scales relevant to macrophytes are reviewed in this special issue (Burnett and Gaylord, 2022).

Features of macrophytes that affect the hydrodynamic forces they experience

Ambient water currents and waves impose hydrodynamic forces on benthic macrophytes that can deform or break them. Measurements of forces on macroalgae, seagrass, and physical models (techniques reviewed in Burnett and Gaylord, 2022) in the field and in flumes in which flow measured in the field is mimicked (velocity profile above the substratum, turbulence spectrum, and wave period and amplitude are matched; techniques described in Koehl and Reidenbach, 2008; Koehl *et al.*, 2013) have revealed how the sizes, shapes, and mechanical properties of seaweeds affect the forces that they experience in flowing water. Mathematical models of how flexible structures of idealized shapes interact with moving fluids also reveal the parameters that affect the hydrodynamic forces they experience (reviewed by Gosselin, 2019).

Hydrodynamic forces on macrophytes

Drag (D) is the hydrodynamic force pushing a body in the same direction as water is flowing relative to the body. Drag on a macrophyte is due to the pressure difference between its upstream and downstream surfaces when a wake forms behind it (form drag), and to the viscous resistance of the water along its surfaces to being sheared (skin friction drag) (Vogel, 1994):

$$D = 0.5\rho C_D U^2 S \qquad (1)$$
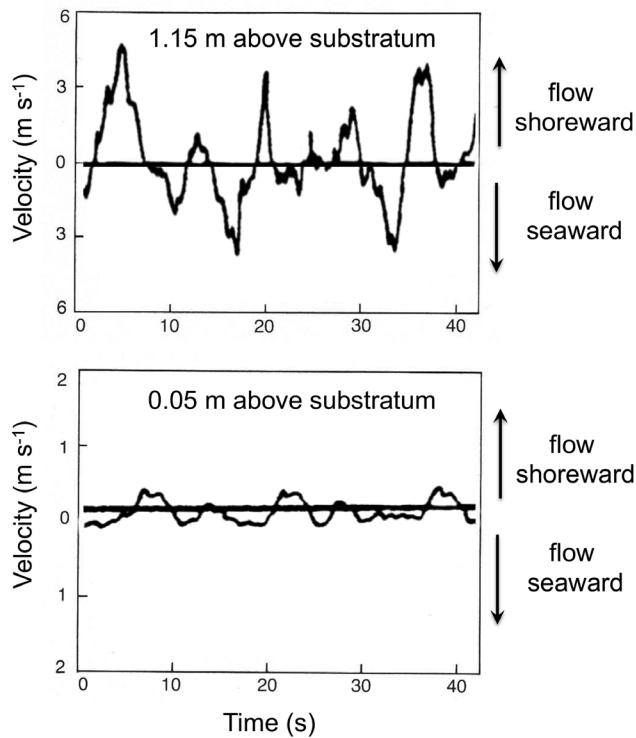
Fig. 4. Water velocity (measured by an EPCO 6130 electromagnetic flowmeter) plotted as a function of time just shoreward of breaking waves in a surge channel (pictured in Fig. 5) on the rocky shore of Tatoosh Island, WA, USA. During each wave, water surged into the channel and then washed back out, so with each wave the water depth varied. Macroalgae (*Laminaria setchelli*) were growing on the side walls of the channel. Data shown in the upper graph were gathered when the probe was positioned in the middle of the surge channel at the height of these *L. setchelli* (1.15 m above the bottom of the surge channel) and was gathered at a time in the tidal cycle when the probe would not be exposed to air (i.e. the probe was ~10 cm below the air–water interface at the end of the backwash of water out of the channel). The lower graph shows velocities near the substratum (0.05 m above at the bottom of the channel). The wave period in this example is ~8 s. The smaller rapid fluctuations in velocity are due to swirling turbulent eddies of a range of sizes that stir the water. (Plots drawn using data from Koehl, 1976.).

where ρ is fluid density, C_D is the drag coefficient (which depends on morphological features such as shape and surface texture), U is the water velocity relative to the macrophyte, and S is planform area of the organism. Since velocities fluctuate in turbulent ambient currents, the instantaneous magnitude of the drag on a macrophyte also varies. For rigid benthic organisms, drag increases with size, both because taller bodies encounter faster flow (Fig. 4) and because S is bigger.

Macrophytes can also experience lift (L), the hydrodynamic force acting at right angles to drag (Vogel, 1994):

$$L = 0.5\rho C_L U^2 S \qquad (2)$$

where C_L is the coefficient of lift. If the flow is faster along one side of an organism than the other (due to an asymmetric

shape or as vortices are shed), it can be sucked sideways or vertically.

Macrophytes attached to surfaces exposed to waves encounter back and forth water motion. Thus hydrodynamic forces can rapidly change in magnitude and direction. A quasi-steady approach is used to calculate instantaneous drag (D_t) and lift (L_t) on an organism in waves using the instantaneous water velocity relative to the organism (U_t). Organisms in the accelerating flow in waves are also subjected to acceleration reaction force (A),

$$A_t = \rho C_M (dU/dt)_t V \qquad (3)$$

where A_t is the instantaneous acceleration reaction, C_M is the inertia coefficient (which depends on organism shape and size, and on wave period), $(dU/dt)_t$ is the instantaneous water acceleration relative to the organism, and V is the volume of water displaced by the organism (Koehl, 1977; Denny *et al.*, 1985; Denny, 1988). When water accelerates past an organism, A_t acts in the same direction as drag, but when water decelerates relative to a body, A_t acts in the opposite direction as drag. Since A_t is proportional to organism volume, it should increase at a greater rate than drag or lift (proportional to area) as an organism grows (Denny *et al.*, 1985). However, A_t is unlikely to limit the size of wave-swept macrophytes for two reasons: (i) many macrophytes have thin blades or leaves, so their volume and area increase at roughly the same rate as they grow; and (ii) the very high accelerations in the surf zone occur on spatial scales much smaller than the macrophytes (Gaylord, 2000).

The instantaneous net force on a benthic organism in turbulent or wavy flow is the vector sum of the acceleration reaction, drag, and lift at that instant (Koehl, 1977, 1984; Denny *et al.*, 1985; Denny, 1988). However, if a wave breaks onto a macrophyte that is not submerged, the transient impingement force can be much larger than the hydrodynamic forces experienced by submerged organisms (Gaylord, 2000; Denny and Gaylord, 2002; Gaylord *et al.*, 2008). Thus, in the coastal habitats of marine macrophytes, the hydrodynamic forces they experience fluctuate rapidly and depend on the tidal height at the moment.

Macrophyte flexibility, size, and shape affect hydrodynamic forces

The morphological and mechanical traits of macrophytes can alter the hydrodynamic forces they experience. Any feature that lowers water velocity and acceleration relative to a benthic macrophyte, or that reduces the size of the wake that forms behind it, can reduce hydrodynamic forces. The flexibility of macrophytes can have all these effects.

Flexible macrophytes are bent over by ambient flow (Fig. 5A). This can move them closer to the substratum where flow velocities are lower (Koehl, 1986, 2000). Very flexible algae that are bent over onto the substratum have a further reduction in
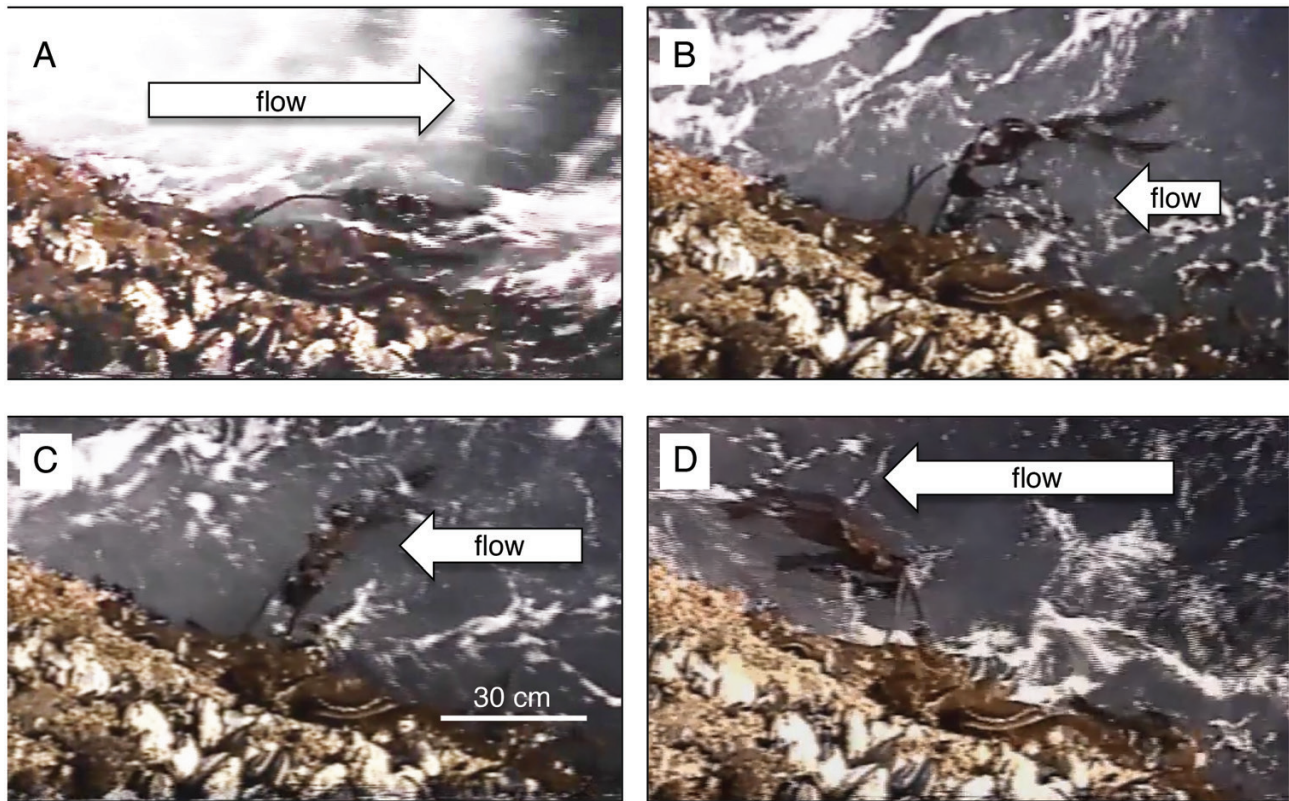
Fig. 5. Frames of a video of the intertidal seaweed, *Laminaria setchelli*, as it sways back and forth in the surge and backwash of a broken wave (see Fig. 3) in the channel where the flow velocities shown in Fig. 4 were recorded. White arrows indicate the instantaneous flow directions and relative magnitudes. (A) Water washes shoreward and flows relative to the kelp, which is bent over and fully extended in the direction of flow. (B and C) Kelp is moving with the water as it flows back seaward. (D) Water rushes seaward and flows relative to the kelp, which is bent over and fully extended in the direction of flow.

drag because only their upper surface is exposed to rapidly flowing water (Koehl, 1984, 2000). Plate-like objects such as algal or seagrass blades form much smaller wakes and experience lower drag when oriented parallel, rather than normal, to the flow direction, so when a macrophyte blade is bent over parallel to ambient flow, its drag coefficient is reduced (Charters *et al.*, 1969; Koehl and Wainwright, 1977; Koehl, 1984, 1986; Carrington, 1990; Koehl *et al.*, 2001; Fonseca *et al.*, 2007; Dijkstra and Uittenbogaard, 2010; Zhang and Nepf, 2020).

A flexible macrophyte can be passively reconfigured by moving water into a streamlined shape that reduces wake size and form drag as ambient flow velocity increases (macroalgae: Koehl, 1984, 1986; Koehl and Alberte, 1988; Carrington, 1990; Martone *et al.*, 2012; de Bettignies *et al.*, 2013; aquatic plants: Bouma *et al.*, 2005; Zhang and Nepf, 2020). Thus, the C_Ds measured for diverse species of flexible macroalgae are low (0.01–0.5) (Koehl, 2000). Macroalgae of different morphologies (degree of branching, thallus thickness, length and density of papillae) can be folded into compact shapes that have low C_Ds at high water speeds (Carrington, 1990), and multiple blades, leaves, or branches on a macrophyte can be

clumped together by the ambient flow into a streamlined bundle where some of them are sheltered from the moving water (macroalgae: Koehl and Alberte, 1988; Koehl *et al.*, 2008; aquatic plants: Fonseca *et al.*, 2019; Zhang and Nepf, 2020). Flexible blade-like algae can reconfigure more readily than whip-like or tree-like forms, and show more effective force reduction as flow speeds rise (Boller and Carrington, 2007). An index of the drag reduction due to such reconfiguration by a flexible organism is the 'figure of merit', which is the slope of a log–log plot of speed-specific drag (D/U^2) as a function of velocity (Vogel, 1984, 1989). The larger the absolute value of the negative slope of such a plot, the greater the relative drag reduction that occurs as velocity increases. Figures of merit for a variety of macroalgae and aquatic vascular plants range from −0.3 to −1.5 (Koehl, 2000; Harder *et al.*, 2006; Zhang and Nepf, 2020).

Flexibility can sometimes lead to an increase in hydrodynamic forces if the blades of macrophytes flutter like flags, or if their stipes or stems wobble from side to side in flowing water. Such motions are due to transient lift forces as vortices are shed into the wake (Denny, 1988; Vogel, 1994; Gosselin, 2019) and to turbulent velocity fluctuations (Koehl *et al.*,

2001). Such wobbling and fluttering increase wake size and form drag (Koehl and Alberte, 1988; Johnson and Koehl, 1994; Koehl *et al.*, 2008).

In the oscillatory flow of waves, flexibility can either increase or decrease the forces on a macrophyte, depending on its length relative to the distance the water flows in a wave before reversing direction. Hydrodynamic forces depend on water velocity and acceleration relative to a body. As a flexible macrophyte is flapped back and forth in wavy flow, it moves with the water (hence there is no flow relative to its surfaces) until it reaches the end of its tether and the water moves past it (Fig. 5). Only those portions of a macrophyte that are fully extended in the direction of flow and experiencing relative water motion are subjected to hydrodynamic forces that pull on its tissues and the holdfast or roots attaching it to the substratum. A short macrophyte reaches the end of its rope early in a wave cycle when velocities and accelerations are high (Fig. 4), whereas longer macrophytes become fully strung out in the direction of flow when the water has begun to decelerate and forces are lower (macroalgae: Koehl, 1984, 1986, 1999; Johnson and Koehl, 1994; seagrass: Koch *et al.*, 2006). If the length of a flexible macrophyte is greater than half the distance that the water moves in a wave before it reverses direction, the macrophyte can move with the water during the entire wave cycle, so further growth in length may not lead to an increase in force, as shown by measurements of forces on kelp trimmed to different lengths on a wave-swept shore (Koehl, 1999).

A flexible macrophyte in wavy flow also experiences a brief inertial force proportional to its mass when it is jerked to a halt as it reaches the end of its tether, and the faster it is moving with the water when suddenly decelerated, the larger this inertial force (Denny and Cowen, 1997; Denny *et al.*, 1998; Gaylord and Denny, 1997). Macrophytes that are jerked to a halt at times during the wave cycle when velocities are highest experience much larger inertial forces than do shorter or longer individuals that are jerked to a halt at times in the wave cycle when the flow is slow (Wolcott, 2007).
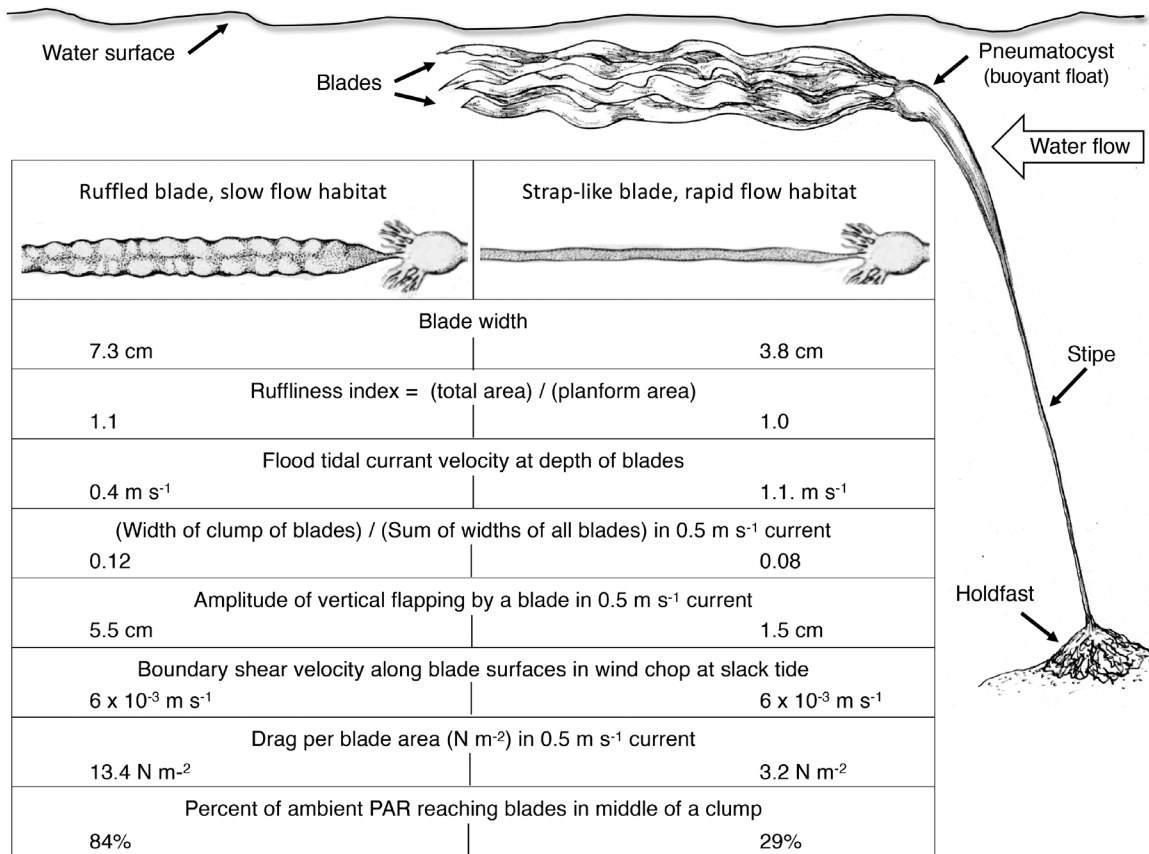
Long, flexible kelp in habitats seaward of breaking waves encounter oscillatory shoreward–seaward water motion as waves pass overhead, but they can also be exposed to alongshore currents that simultaneously push them in a different direction from the waves, thereby reducing the water flow relative to them and the wave forces they experience (Gaylord *et al.*, 2003).

If a flexible macrophyte is long and slender, it can be wrapped around itself and tied into knots as it is moved back and forth by waves or tidal currents, and neighboring algal fronds or grass blades can become entangled with each other. Such knots and tangles have been shown to increase the likelihood that kelp will break in moving water by increasing the hydrodynamic forces on the kelp, and by providing protected microhabitats for herbivores that can damage the kelp (Koehl and Wainwright, 1977; Burnett and Koehl, 2018).

When a marine macrophyte grows, it extends into faster flow away from the substratum (higher U and dU/dt) and increases in size (greater S, V, and mass), which generally leads to larger hydrodynamic and inertial forces (Carrington, 1990; Gaylord et al., 1994, 2008; Gaylord and Denny, 1997; Wolcott, 2007). Field studies show that large seaweeds are more likely to be dislodged from the substratum than are small individuals (Black, 1976; Santelices *et al.*, 1980; Dudgeon and Johnson, 1992; Blanchette, 1997; Kawamata, 2001; Wolcott, 2007; de Bettignies et al., 2013, 2015; Burnett and Koehl, 2021). An important caveat to this generalization is that flexible macrophytes can escape from high forces in waves by being very long. Therefore, the effects of a macrophyte's size on the hydrodynamic and inertial forces it experiences in a coastal habitat depend on wave size (which determines U, dU/dt, and the distance water travels before reversing direction). More macrophytes are broken or dislodged during seasonal storms that produce large waves than during periods of small waves (macrolagae: Seymour *et al.*, 1989; Dayton *et al.*, 1992; Johnson and Koehl, 1994; Graham *et al.*, 1997; Filbee-Dexter and Scheibling, 2012; seagrass: Patterson *et al.*, 2001; Congdon *et al.*, 2019). Thus, the consequences of a macrophyte's size on the forces it experiences in nature vary with time because wave sizes vary on the scale of seconds (Fig. 4), on the scale of hours to days as wind conditions change, on the scale of months due to the seasonal frequency of large storms, and on the scale of years due to effects such as El Niño.

Trade-offs between different functions

Macrophyte designs that reduce hydrodynamic forces can also affect the light interception on which photosynthetic performance depends. In general, when flexible macrophytes are bent over into deeper water by ambient currents, the PAR (light of wavelengths used in photosynthesis) arriving at their surfaces is attenuated and they can be shaded by neighboring competitors, but when flexible blades are passively reoriented parallel to flowing water, that also orients their surface area normal to incident light, thereby enhancing photosynthesis (Hurd *et al.*, 1997). One example of a trade-off between light interception for photosynthesis and drag reduction is provided by the blades of macroalgae. Many species have flat blades in rapid-flow habitats, but have ruffled blades at sites exposed to slow flow (reviewed in Koehl *et al.*, 2008). Flat blades collapse into a streamlined bundle in flowing water, but suffer self-shading that reduces their photosynthetic rate, whereas ruffled blades are moved around erratically and remain spread out in flowing water, so they experience high drag, but little self-shading (Koehl and Alberte, 1988) (Fig. 6). Blade growth patterns that produce these different shapes are induced by the magnitude of tensile stress in blade tissues due to hydrodynamic force (Koehl and Silk, 2021).

Ruffled blade, slow flow habitat	Strap-like blade, rapid flow habitat
Blade width	
7.3 cm	3.8 cm
Ruffliness index = (total area) / (planform area)	
1.1	1.0
Flood tidal currant velocity at depth of blades	
0.4 m s^{-1}	1.1. m s^{-1}
(Width of clump of blades) / (Sum of widths of all blades) in 0.5 m s^{-1} current	
0.12	0.08
Amplitude of vertical flapping by a blade in 0.5 m s^{-1} current	
5.5 cm	1.5 cm
Boundary shear velocity along blade surfaces in wind chop at slack tide	
6 x 10^{-3} m s^{-1}	6 x 10^{-3} m s^{-1}
Drag per blade area (N m^{-2}) in 0.5 m s^{-1} current	
13.4 N m^{-2}	3.2 N m^{-2}
Percent of ambient PAR reaching blades in middle of a clump	
84%	29%

Fig. 6. Comparison of the morphology, flow habitat, and performance of ruffled versus strap-like blades of the bull kelp, *Nereocystis leutkeana* (mean values of data in Koehl and Alberte, 1988). The blades of the kelp are held near the water surface by a gas-filled pneumatocyst and are passively reoriented parallel to ambient water currents. The 'ruffliness index' of a blade is a measure of how much greater the actual area of the blade is relative to its planform area (a flat blade has a ruffliness index of 1). When ruffled and strap-like blades are exposed to the same ambient water flow, ruffled blades flutter at greater amplitude, but the up and down speeds through the water as they flap are the same for both blade morphologies, as are the boundary shear velocities along their surfaces (which affect uptake of dissolved materials from the water). However, low amplitude fluttering and the ability of strap-like blades to collapse together into a streamlined bundle (i.e. the ratio of the width of the clump to the sum of the widths of all the blades in the clump is low) result in lower drag force per blade area than experienced by ruffled blades at the same flow velocity. The ability of ruffled blades to remain spread out in flowing water, along with their erratic, high-amplitude fluttering that enhances light flecking in the clump, results in much less self-shading (i.e. the percentage of ambient photosynthetically active radiation, PAR, reaching blades in the middle of a clump is higher) than experienced by strap-like blades in the same ambient flow.

The rates of uptake of essential substances and removal of wastes along surfaces of marine macrophytes depend on the water velocity relative to those surfaces. Therefore, physiological processes such as photosynthesis are inhibited if those relative velocities are below a critical saturation velocity (macroalgae: Hurd, 2000; seagrass: Koch *et al.*, 2006). Features of macrophytes that reduce relative flow to below saturation velocities can worsen physiological performance while improving hydrodynamic force reduction. In contrast, fluttering by macrophyte blades that increases drag can also raise the photosynthetic rate in slow currents that are below saturation velocity via two mechanisms: (i) increasing the velocity of water relative to blade surfaces; and (ii) stirring the water near blades, thereby replacing depleted water near the blades with undepleted water (e.g. macroalgae: Koehl and Alberte, 1988; seagrass: Koch *et al.*, 2006). Thus, the most effective designs for balancing these trade–offs between avoiding hydrodynamic

damage and enhancing photosynthetic performance depend on the flow habitats of macrophytes.

The stems of marsh plants and seagrasses provide another example of trade-offs between different functions. Aquatic plants with stiff, strong stems can withstand waves better than can those with flexible, weak stems, but when intertidal plants are exposed to air, those with very flexible stems lie flat on the wet sediment and suffer less dessication than do upright plants with stiff stems (Coops and Van der Velde, 1996; Bouma *et al.*, 2009).

Features of macrophytes that affect their deformation and breakage in ambient water flow

Mechanical stress in a structure (organism) is the force per cross-sectional area of material (tissue) bearing the force. The

size and shape of a macrophyte determine the magnitude and distribution of stresses in its tissues when it is subjected to mechanical loads such as hydrodynamic forces, while the mechanical properties of its tissues ('material properties') determine how much it deforms and whether or not it breaks when subjected to those stresses. Techniques for using engineering structural analysis and materials science to study the functional morphology of macrophytes are described by Koehl and Wainwright (1986). I have reviewed research using these biomechanical approaches to identify which features of marine macrophytes determine their deformation and breakage in ambient water flow (Koehl, 1986, 2000; Koehl et al., 2001, 2003), so here I will instead report some examples that illustrate the importance of field studies to discovering how the structural design of marine macrophytes affects their performance in nature.

Temporal patterns of forces experienced by marine macrophytes affect performance

The deformation and breakage of macrophytes depend on the temporal patterns of loading they experience in their natural habitats, so field measurements of the time course of hydrodynamic forces on macrophytes are critical to understanding their biomechanical performance. Material properties of macrophyte tissues can depend on the rate at which they are deformed (Johnson and Koehl, 1994; Hale, 2001; Harder et al., 2006; Denny et al., 2013; Burnett and Koehl, 2021), so laboratory measurements of their stiffness, extensibility, resilience, strength, or toughness should mimic the deformation rates and load durations they experience in the field. For example, when macrophytes attached to the substratum by tethers composed of very extensible tissue are exposed to transient high loads like those they experience in turbulent currents or waves, the tissue may not be stretched far enough to reach its breaking stress before the pulse of force is over (Koehl and Wainwright, 1977; Hale, 2001; Burnett and Koehl, 2021). Therefore, extensible kelp stipes act as shock absorbers whose stretching absorbs mechanical work so kelp can survive brief pulses of high loads. Marine macrophytes exposed to turbulent currents or waves experience repetitive pulses of force thousands of times per day. Even if a single pulse of force is not sufficient to break the organism, its tissues can accumulate small cracks that eventually can lead to fatigue fracture. Determining the repetitive hydrodynamic loads on macrophytes in the field informs research into how tissue microarchitecture resists fatigue fracture (Hale, 2001; Mach, 2009; Denny et al., 2013).

Different designs can perform well in the same biophysical habitat

There is no single optimal design for surviving in a particular hydrodynamic environment, as evidenced by the great diversity of macrophytes living side by side on the shore (Fig. 1B). For example, macroalgal tissue can be tough (i.e. require a lot of mechanical work per volume to break) either by being stiff

(high elastic modulus) and strong (high breaking stress), or by being weak (low breaking stress) but very extensible (high breaking strain) (Koehl, 2000). Different species of algae living at the same site can resist similar hydrodynamic loads, either by having slim stipes composed of strong tissue, or by having wide stipes with weak tissue (Dudgeon and Johnson, 1992). Stresses in the stipes of upright macroalgae that are bent by a hydrodynamic force are much greater than stresses in rope-like macroalgae that are pulled by the same load, so species that bear tensile loads can withstand larger hydrodynamic forces than can species that are bent by flowing water (Koehl, 1986, 2000). Similarly, some aquatic vascular plants avoid large hydrodynamic forces by being very flexible ('avoidance strategy') while others are stiff and strong enough to resist breakage by flowing water ('tolerance strategy') (Coops and Van der Velde, 1996; Puijalon et al., 2011).

Macroalgae and seagrass can support their photosynthesizing blades higher in the water column to enhance access to light either by having stiff stems or stipes or by being buoyant (macroalgae: Stewart, 2004, 2006a, b; Stewart et al., 2007; Burnett and Koehl, 2017; seagrass: Luhar and Nepf, 2011). Macrophytes using buoyancy are easily pushed over by pulses of rapid flow, but rapidly rebound to their upright posture, whereas stiff individuals do not move as readily with the flow (macroalgae: Stewart, 2004, 2006a, b; Burnett and Koehl, 2017; seagrass: Luhar and Nepf, 2011). In addition, the gas-filled floats ('pneumatocysts') on buoyant macroalgae help to keep their branches spread out and reduce shading in aggregations of seaweeds (Stewart et al., 2007; Burnett and Koehl, 2017). However, pneumatocysts on branching seaweeds interfere with their reconfiguration into a drag-reducing streamlined shape in flowing water (Stewart, 2006b).

Field studies revealed that macrophytes with 'bad' mechanical designs according to engineering criteria can be successful in mechanically stressful environments if they have life history strategies tuned to temporal changes in environmental conditions. For example, many species of macroalgae grow quickly in the summer to large size (and thus higher hydrodynamic force) and have weak tissues, but they reproduce before seasonally predictable storms occur that rip them off the shore (Johnson and Koehl, 1994; Koehl, 1999; Wolcott, 2007). In contrast, other species of macroalgae grow slowly, have strong tissues, reproduce later, and can regrow new fronds if pruned by winter waves (Koehl, 1999; Burnett and Koehl, 2018, 2019). Both strategies are very successful on wave-swept shores.

Some macrophytes utilize 'bad' engineering designs to enhance their reproduction and dispersal. For example, as the tropical alga, *Turbinaria ornata*, grows bigger and becomes reproductively mature, its stipe tissue weakens and it becomes more buoyant. These mature algae break more readily in storms than do non-reproductive juveniles, and form floating aggregations where they shed gametes and are transported to new sites by currents (Stewart, 2006c). The eelgrass, *Zostera marina*, uses a similar strategy for long-distance dispersal. Seagrasses reproduce asexually by developing new shoots along growing rhizomes,

and sexually via water–dispersed filamentous pollen that is captured by flowers on reproductive shoots (Ackerman, 1997*a*, *b*). Reproductive shoots remain buoyant, but the breaking stress of their stems decreases as the seeds mature, so floating rafts of broken-off seed-bearing shoots form and are transported great distances (>100 km) by ambient currents (Harwell and Orth, 2002; Källströma *et al.*, 2008). However, eelgrass live in habitats subjected to hurricanes. A few of the reproductive shoots they produce have very high breaking strength and toughness, enabling them to persist during severe storms while the rest of the population is washed away (Patterson *et al.*, 2001).

Phenotypic plasticity

Many species of macroalgae are distributed across a range of water flow habitats. Some species have tougher, stronger tissues and/or have thallus morphologies that reduce hydrodynamic forces and tissue stresses when they are in high-flow environments than they do in more protected habitats (Armstrong, 1988; Koehl and Alberte, 1988; Holbrook *et al.*, 1991; Lowell *et al.*, 1991; Johnson and Koehl, 1994; Hurd *et al.*, 1996; Hurd, 2000; Koehl *et al.*, 2008; Bekkby *et al.*, 2014; Koehl and Silk, 2021). Experimental manipulations of physical conditions and field transplant experiments show that these differences in tissue composition and thallus shape can be due to phenotypic plasticity (Kraemer and Chapman, 1991; Lowell *et al.*, 1991; Koehl *et al.*, 2008; Burnett and Koehl, 2018; Koehl and Silk, 2021). Such plasticity permits macrophytes to adjust their mechanical design and performance in response to cues from the physical environment.

Aquatic plants also show phenotypic plasticity in response to environmental conditions (reviewed by McMahon *et al.*, 2013; Maxwell *et al.*, 2014; McDonald *et al.*, 2016; Chiara *et al.*, 2021; Pazzaglia *et al.*, 2021; Soissons *et al.*, 2021). For example, plants exposed to high wave action produce shorter stems and have lower flexural stiffness (reducing hydrodynamic forces), and have a higher ratio of root to shoot biomass (enhacing anchoring in the sediment) than do plants exposed to slower flow (Coops and Van der Velde, 1996; Silinski *et al.*, 2018; Cao *et al.*, 2020). Another example of a morphological response by seagrass to the flow environment is that internodal distances between new shoots along rhizomes are longer at the edges of seagrass beds exposed to rapid water motion than they are in regions of the beds that are shielded from fast flow (Jensen and Bell, 2001). This response produces more rapid expansion of seagrass beds in the upstream direction where flow is fastest.

Breakage in variable environments

As described above, the hydrodynamic forces experienced by a macroalga or seagrass fluctuate rapidly in turbulent flow and waves, vary on scales of hours and days as the tides come and go and the weather changes, and differ seasonally as the frequency of storms changes. A macrophyte is broken or ripped off the shore if the stress in its tissues caused by hydrodynamic force exceeds that tissue's breaking strength. The safety factor of a component of an organism (e.g. the stem or stipe of a macrophyte) is the ratio of the strength of the tissue of the component to the peak stress that it experiences during its lifetime (Alexander, 1981). Biological structures that experience highly variable loads tend to have higher safety factors than do those facing more predictable forces (Alexander, 1981). Denny (2006) developed statistical methods for using wave data to predict peak water velocities and accelerations on a site at the shore, which are used to calculate maximal hydrodynamic forces on organisms living there. He found that diverse organisms living on wave-beaten shores tend to have high safety factors.

Field studies of macrophytes show that their size, shape, and material properties change with age and differ between sites exposed to different water flow regimes. Therefore, we use 'environmental stress factor' (ESF) rather than safety factor to describe the likelihood that a marine macrophyte will be broken or washed away. ESF is the ratio of the tissue strength (stress required to break the tissue) of a component of an organism at some stage in its life to the maximum stress experienced by that component as it functions in the habitat of the organcism during that life stage (Johnson and Koehl, 1994). The kelp *Nereocystis luetkeana* (Fig. 1A) modifies blade shape (affecting drag), stipe morphology (affecting stress), and tissue strength such that the ESF is the same in different hydrodynamic environments (Johnson and Koehl, 1994). ESF can change during the life of a macrophyte, and low ESF correlates with the times that macrophytes break or wash away (Johnson and Koehl, 1994; Stewart, 2006*c*; Wolcott, 2007; Sirison and Burnett, 2020).

Ecological interactions of macrophytes can affect their mechanical performance in ambient water flow

Marine macrophytes interact with each other, with epibionts living on them, and with herbivores. These ecological interactions, which vary with time and location, can affect the biomechanical performance of macrophytes in their natural habitats.

Living in aggregations

Although many studies of macrophyte hydrodynamic and biomechanical performance have been carried out on isolated individuals, marine macrophytes often occur in single or multispecies aggregations such as kelp forests (Fig. 1A), intertidal algal beds (Fig. 1B), and seagrass meadows (Fig. 2). Physical conditions that macrophytes encounter within such groups are different from those experienced by isolated individuals. Macroalgae or plants within a macrophyte bed can shade each other (Black, 1974; Holbrook *et al.*, 1991; Stewart

et al., 2007) and reduce the transport of water-borne materials such as nutrients, gases, wastes, and propagules (Jackson and Winant, 1983; Gaylord et al., 2007, 2012), but also can protect each other from rapid water flow and high hydrodynamic forces.

Water flow in beds of aquatic macrophytes has been analyzed using similar approaches to those developed to quantify effects of terrestrial forests and crops on wind (e.g. Nowell and Jumars, 1984; Monteith and Unsworth, 2013). Flow around and through macroalgal and seagrass beds has been studied via field measurements, flume experiments with living macrophytes or physical models, and mathematical models (reviewed for macroalgae: Hurd, 2000; for aquatic plants: Nepf, 1999; Koch et al., 2006; Fonseca et al., 2019). Water velocities are reduced in kelp forests (Jackson and Winant, 1983; Eckman et al., 1989; Koehl and Alberte, 1988; Jackson, 1997; Hurd, 2000; Gaylord et al., 2007) and meadows of aquatic plants (Eckman, 1983; Nepf, 1999; Koch et al., 2006; Fonseca et al., 2019). Macrophyte canopies also damp waves (Elwany et al., 1995; Dubi and Tørum, 1996; Mork, 1996; Chen et al., 2007; Lei and Nepf, 2019; Zhua et al., 2021).

The water velocity profile within a stand of macrophytes depends on the distribution, morphology, and flexibility of blades or leaves on the macrophytes (Nepf, 1999; Lei and Nepf, 2019), and on the size, density (number of thalli or shoots per area of substratum), and spatial arrangement of the individuals in the bed (macroalgae: Gaylord et al., 2012; aquatic plants: Nepf, 1999; Fonseca et al., 2019). For example, if the density of a seagrass bed is high, water is diverted around and above the canopy (Fig. 7), and the steep velocity gradient between the slow flow in the canopy and rapid flow above it produces vortices that enhance the exchange of mass and momentum between the canopy and the water flowing above it (Gambi et al., 1990; Worcester, 1995; Koch and Gust, 1999; Nepf, 1999). Such 'skimming' overflow, which is especially pronounced for flexible plants that are bent over by the flow and pushed together into a compact layer (Fig. 7B, C), reduces flow-induced shear on the substratum, resulting in greater stability of the sediment where seagrass roots are anchored (Fonseca et al., 2019). However, small-scale flow around an individual plant stem can cause local water motion into and out of the sediment (Koch et al., 2006) and sediment scouring around the
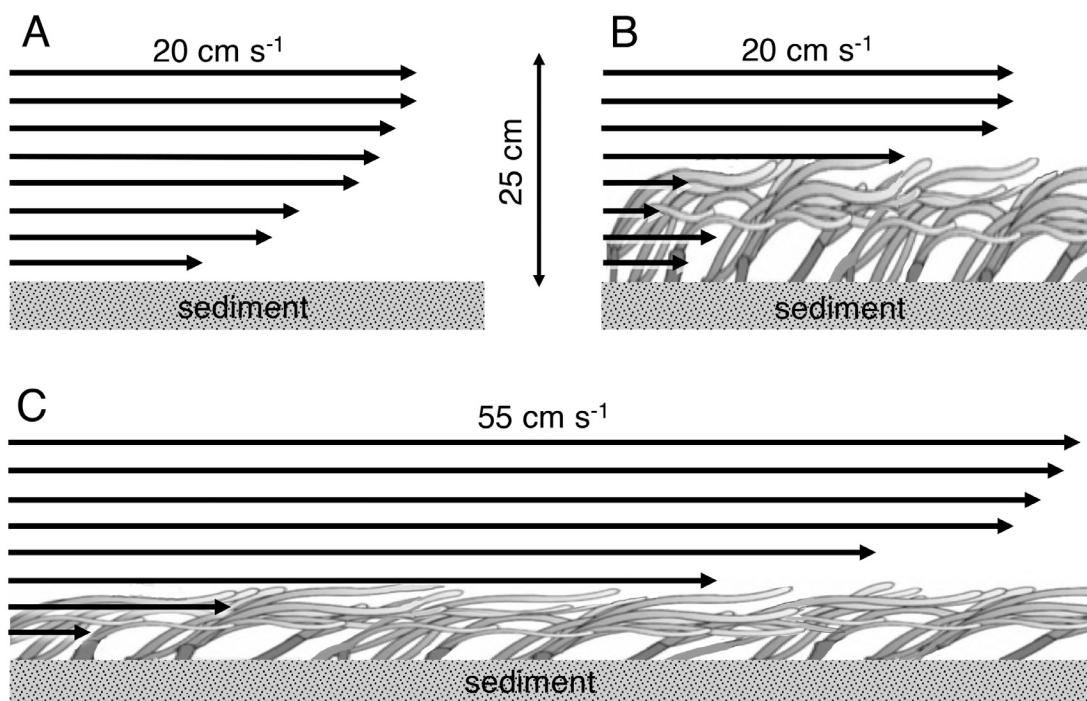
Fig. 7. Diagram of water velocity profiles near and within a seagrass bed (based on descriptions in Nowell and Jumars, 1984; Koch et al., 2006; Monteith and Unsworth, 2013; and data in Fonseca et al., 2019). Arrows indicate mean velocities at different heights above the substratum. Flow in marine habitats is turbulent, so swirling eddies (not shown in the diagram) exchange mass and momentum between adjacent streamlines. (A) Water velocity profile over the sediment at a position 25 cm upstream of a bed of seagrass. (B) Water velocity profile within and above a seagrass bed at a position 50 cm downstream from the upstream edge of the bed exposed to a current of 20 cm s^{-1}. Near the top of the canopy where the leaves are pushed together by the flow, there is more resistance to water motion than lower in the canopy where the stiffer stems have more space between them. There is a steep velocity gradient at the top of the canopy that produces vortices (not shown in the diagram) that enhance the exchange of water between the canopy and the current flowing above it. (C) Water velocity profile within and above a seagrass bed at a position 50 cm downstream from the upstream edge of the bed exposed to a current of 55 cm s^{-1}. When exposed to faster flow, canopy height is reduced as plants are pushed down closer to the substratum, flow within the seagrass bed is greatly reduced, and a very steep velocity gradient develops at the top of the canopy.

base of the stem (Bouma *et al.*, 2009). Ambient flow above a critical velocity (which depends on seagrass size, spacing, and stiffness) can produce waves of synchronous blade bending that ripple across a seagrass bed and enhance stirring of water into the canopy ('monami' is the aquatic version of 'hunami', the waves of bending that sweep across, for example, wheat fields in the wind) (Grizzle *et al.*, 1996; Singh *et al.*, 2016).

Hydrodynamic forces and flow-mediated transport experienced by an individual macrophyte depend on its distance from the upstream edge or side of the bed, its proximity to gaps in the aggregation, and the spatial arrangement of its neighbors (macroalgae: Koehl and Alberte, 1988; Gaylord *et al.*, 2007; seagrass: Fonseca et al., 2007, 2019). Hydrodynamic forces measured on individual macroalgae or seagrass plants are lower when they are in the middle of a macrophyte bed than at the edge, or are standing alone (macroalgae: Johnson, 2001; Gaylord *et al.*, 2007; Stewart *et al.*, 2007; seagrass: Fonseca *et al.*, 2019). In some cases, neighbors within a densely packed aggregation can support each other mechanically. For example, intertidal kelp, *Postelsia palmaeformis* (Fig. 1B), that grow tall in light-limited aggregations can remain upright by leaning on each other (Holbrook *et al.*, 1991). Although transport is slowed within aggregations, the wakes of macrophytes can alter temporal scales of turbulence (macroalgae: Anderson and Charters, 1982; aquatic plants: Ackerman and Okubo, 1993; Nepf, 1999) and can sometimes increase dispersion of water-borne materials (macroalgae: Koehl *et al.*, 1993; seagrass: Worcester, 1995), and induce vertical flow (seagrass: Nepf and Koch, 1999).

Because macrophyte beds alter the physical environment, studies of individual thalli or shoots isolated from their neighbors may not provide useful insights about their performance in nature. Rather, the physical conditions actually encountered by an individual within a macrophyte bed must be measured in order to design ecologically relevant laboratory studies of biomechanical performance. Furthermore, the structure of macrophyte beds changes seasonally as individuals recruit, grow, are pruned by herbivores and breakage, and are swept away or die. Therefore, the timing of the field measurements must be matched to the ages of the individuals being studied in the lab.

Effects of epibionts on biomechanical performance

Macroalgae and seagrasses provide surfaces on which other organisms live (reviewed by, for example, Seed and O'Connor, 1981; Koch *et al.*, 2006; Harder, 2008; Wahl, 1989, 2008; Christie *et al.*, 2009). The epibionts living on macrophyte hosts include bacteria, micro- and macroalgae, sessile suspension-feeding invertebrates such as byrozoans and sponges, and motile fauna such as snails and crustaceans. Epibionts are more abundant on macroalgae that have multiple branches or blades, occur in dense aggregations, or become tangled (Norderhaug and Christie, 2011; Arnold *et al.*, 2016; Teagle *et al.*, 2017; Burnett and Koehl, 2018). Such structural complexity provides refuges for animals where they are protected from water flow

that could sweep them away (Fenwick, 1976; Duggins *et al.*, 2001; Burnett and Koehl, 2019). Epibiont cover on seagrasses is greatest on the oldest leaves around the periphery of a shoot, and epibionts are shed as these weakened leaves break off in ambient currents (de los Santos *et al.*, 2012.

Epibionts have two important biomechanical consequences for their macrophyte hosts: (i) they interfere with mass transport between macrophyte surfaces and the surrounding water, and (ii) they increase the likelihood that a macrophyte will break or be swept away by ambient water flow. Epibionts can decrease the exchange of dissolved nutrients, gases, and wastes between macroalgae or seagrasses and the surrounding water, both by covering host exchange surfaces and by depleting the substances from the water (Wahl, 1989; Hurd *et al.*, 2000; Koch *et al.*, 2006; da Gama *et al.*, 2014; Harder, 2008). One way in which epibionts raise the probability of macrophyte dislodgement by flowing water is by increasing the effective size or stiffness of the host on which they are sitting, thereby increasing the hydrodynamic forces the host must bear (Koch *et al.*, 2006; Harder, 2008; Wahl, 2008; Anderson and Martone, 2014). In addition, epibionts can contribute to host breakage by affecting the mechanical properties of underlying host tissues (e.g. reducing tissue strength, extensibility, or toughness) (Wahl, 1989; Krumhansl *et al.*, 2011). Herbivores that graze on epiphytic algae can reduce these deleterious effects on the host macroalga or plant (Hughes *et al.*, 2004; Heck and Valentine, 2006), whereas wounds produced by herbivores that eat host tissues can increase the risk of breakage.

Effects of herbivores on biomechanical performance

Marine macrophytes are wounded by benthic grazers such as sea urchins, swimming herbivores such as fish, and by herbivorous epibionts such as gastropods and crustaceans (Fig. 8) (macroalgae: Burnett and Koehl, 2019; seagrass: Scott *et al.*, 2018). Although the biomechanical consequences of grazing on macroalgae have been well studied, less is known about the biomechanics of herbivory on seagrass. Grazing can have little impact on seagrass population density, can improve photosynthetic performance by removing epiphytes, and can affect the demography of seagrass populations if herbivores prefer young shoots or eat seeds (reviewed by Heck and Valentine, 2006; Valentine and Duffy, 2006). Species of seagrass that invest in toughening their leaves, which have high fiber content and carbon to nitrogen ratios, are less susceptible to herbivores (de los Santos *et al.*, 2012).

When macroalgae are subjected to hydrodynamic forces, they often break at the holes, scratches, and gouges produced by herbivores (Black, 1976; Koehl and Wainwright, 1977; Santelices *et al.*, 1980; Biedka, 1987; Denny *et al.*, 1989; Lowell *et al.*, 1991; Hughes, 2010; de Bettignies *et al.*, 2012; Burnett and Koehl, 2018, 2019). The biomass of algae lost from a community due to such breakage can exceed the loss due to consumption by herbivores (Koehl and Wainwright, 1977; Padilla,
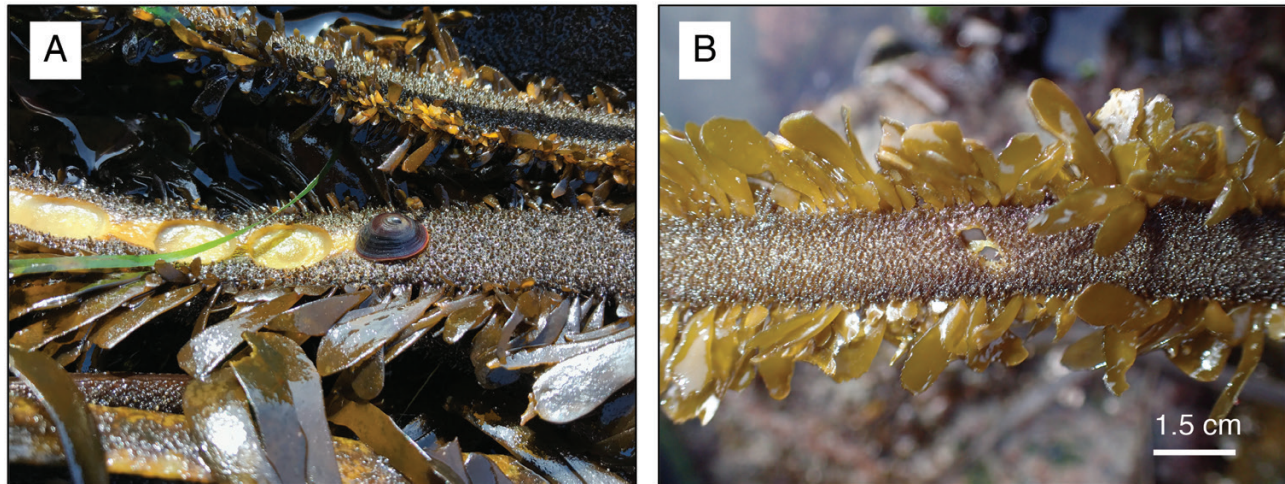
Fig. 8. Examples of wounds produced by grazing epibionts on the rachis of fronds of the intertidal kelp, *Egregia menziesii*. (A) The limpet *Lottia insessa*. (B) An amphipod (seven genera of amphipods chew burrows into rachis tissue, Burnett and Koehl, 2018) (photos by Nicholas Burnett).

1993). The cross-sectional area of the section of a frond where a grazer has removed tissue is reduced, so the stress in that region due to hydrodynamic forces on the frond is increased. In addition, very high stresses develop at the tips of cracks when a structure bears a force (Wainwright *et al.*, 1976), so herbivores that make sharp cuts and scratches in a macrophyte can cause such local stress concentration. If a force on a frond produces a local stress at the herbivore wound that exceeds the strength of the tissue, the frond breaks. However, features of macroalgal tissues, such as calcification or the arrangement of fiber-reinforced cells, can cause the tissue to tear in a preferential direction (akin to ripstop fabric), thereby reducing tissue loss due to wounds made by herbivores (Padilla, 1993).

Herbivore damage can change the size, morphology, and tissue mechanical properties of macrophytes, which in turn can affect their biomechanical performance in flowing water. Breakage at grazer wounds prunes macroalgae to smaller sizes (Black, 1976; Biedka *et al.*, 1987; Denny *et al.*, 1989; de Bettignies *et al.*, 2012; Burnett and Koehl, 2019, 2020). In some cases, such pruning enables perennial kelp to survive winter storms (Black, 1976; Wolcott, 2007; de Bettignies *et al.*, 2012), whereas in other cases pruning by herbivores does not improve overwintering survivorship (Burnett and Koehl, 2020). Some macroalgae respond to wounding by increasing tissue strength (Lowell *et al.*, 1991), while others increase the cross-sectional area of the region that was damaged (Burnett and Koehl, 2019). Wounds and breakage can sometimes stimulate a macroalga to grow new fronds, so the thallus becomes bushier (Sargent and Lantrip, 1952; Black, 1974; Fox, 2013). Even when wounds do not cause pruning, herbivore damage can lower growth rates (O'Brien and Scheibling, 2016; Pfister and Betcher, 2018; Burnett and Koehl, 2020).

Herbivore damage to macrophytes varies in space and time.. For example, herbivory is lower on macroalgae at sites exposed to heavy wave action than on those at protected sites (Smale *et al.*, 2016; Burnett and Koehl, 2017). Grazing pressure tends to be seasonal. Macroalgae have high growth rates during the summer, and the populations of epibiotic herbivores increase dramatically as the algae increase in size (Gunnill, 1983; Winkler *et al.*, 2017; Burnett and Koehl, 2019, 2020). Thus, grazers are more abundant on large, old kelp than on small, young ones (de Bettignies *et al.*, 2012; Teagle *et al.*, 2017). In contrast, the number of epibiotic herbivores on macroalgae decreases during the winter when the large waves that wash away epibionts are more frequent (Duggins *et al.*, 2001; de Bettignies *et al.*, 2013; Burnett and Koehl, 2020). In addition, in the late autumn and winter when growth rates are low and waves are big, old macroalgae that have accumulated many wounds tend to be broken more frequently than do younger macroalgae with fewer wounds (Johnson and Koehl, 1994; de Bettignies *et al.*, 2012; Burnett and Koehl, 2019).

Because herbivory rates vary with season and between sites, and because grazer damage can alter the design and hydrodynamic performance of macrophytes, field studies to determine the timing and degree of grazing on macrophytes is an important component of understanding their mechanical ecology.

Conclusions

Field studies of the physical environment, ecological interactions, and life history strategies of marine macrophytes reveal which aspects of their biomechanical performance are important to their success in natural habitats. Measuring how hydrodynamic forces and macrophyte morphology change across a range of temporal and spatial scales in natural environments enables us to design ecologically relevant laboratory experiments to study biomechanical function.

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Conflict of interest

The author has no financial interests or connections, direct or indirect, or other situations that might raise the question of bias in the work reported or the conclusions, implications, or opinions stated, including pertinent commercial or other sources of funding for the author or for the author's department or organization(s), personal relationships, or direct academic competition.

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