REVIEW PAPER

Flow, form, and force: methods and frameworks for field studies of macroalgal biomechanics

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Abstract

Macroalgae are ecologically important organisms that often inhabit locations with physically challenging water motion. The biomechanical traits that permit their survival in these conditions have been of interest to biologists and engineers alike, but logistical and technical challenges of conducting investigations in macroalgal habitats have often prevented optimal study of these traits. Here, we review field methods for quantifying three major components of macroalgal biomechanics in moving water: fluid flow, macroalgal form, and hydrodynamic force. The implementation of some methodologies is limited due to the current state and accessibility of technology, but many of these limitations can be remedied by custom-built devices, borrowing techniques from other systems, or shifting lab-based approaches to the field. We also describe several frameworks for integrating flow, form, and force data that can facilitate comparisons of macroalgal biomechanics in field settings with predictions from theory and lab-based experiments, or comparisons between flow conditions, habitats, and species. These methods and frameworks, when used on scales that are relevant to the examined processes, can reveal mechanistic information about the functional traits that permit macroalgae to withstand physically challenging water motion in their habitats, using the actual fluid flows, macroalgal forms, and physical forces that occur in nature.

Keywords: Ecomechanics, hydrodynamic force, kelp, material properties, safety factor, seaweed.

Introduction

Macroalgae are a diverse group of autotrophs that support rich communities in marine systems by providing food and three-dimensional habitat for other organisms, yet macroalgae often inhabit locations where physical stressors challenge their structural integrity and survival (Koehl and Wainwright, 1977; Blanchette, 1997; Steneck *et al.*, 2002; Graham *et al.*, 2007; Reed *et al.*, 2011; Teagle *et al.*, 2017). Most notably, water motion (e.g. currents or waves) exerts hydrodynamic

forces on macroalgae, which may be damaged or dislodged from the shoreline if the forces are excessively large (Koehl and Wainwright, 1977; Wolcott, 2007; Demes *et al.*, 2013). These two destructive processes are critically important to the ecology and evolution of macroalgae: damage (i.e. tattering, erosion of thalli) removes photosynthetic tissue, resulting in reduced growth, and decreases the provision of habitat and food to other organisms; dislodgement (i.e. entire thalli breaking

from the substratum) removes macroalgae altogether, often resulting in their mortality and loss of valuable habitat and food from the local community (Graham *et al.*, 2007; Demes *et al.*, 2013; de Bettignies *et al.*, 2013b; Burnett and Koehl, 2020).

The biomechanical performance of macroalgae in moving water depends on interactions between water flow patterns, macroalgal forms, and the mechanical forces experienced by the macroalgae, but these basic components of biomechanical performance are also interdependent (Fig. 1). Water motion in macroalgal habitats can change substantially over a range of time scales, from seconds within a wave cycle to weeks or months within a storm season, and over a range of spatial scales, from different locations on a shoreline to different shorelines on a continent (Gaylord, 1999; O'Donnell and Denny, 2008; Mislan *et al.*, 2011; Jensen and Denny, 2015; Burnett and Koehl, 2020). Furthermore, biomechanical performance can depend on instantaneous flow–form–force interactions, such as the immediate response of macroalgae to waves, and long-term interactions, such as the plastic growth of macroalgae over weeks that alters their morphologies and tissue properties in response to the mechanical loads they experience (Denny *et al.*, 1989; Johnson and Koehl, 1994; Wernberg and Thomsen, 2005; Koehl *et al.*, 2008; Coleman and Martone, 2020; Koehl and Silk, 2021; Millar *et al.*, 2021). Thus, the flow–form–force interactions that drive the biomechanical performance of macroalgae are intricate and can be complicated by flow patterns that change appreciably through space and time, and by the large diversity and plasticity of macroalgal forms in nature (Gaylord *et al.*, 1994; Gaylord, 1999, 2000; Fowler-Walker *et al.*, 2006; O'Donnell and Denny, 2008; Koehl *et al.*, 2008; Coleman and Martone, 2020).

The survival of macroalgae in physically challenging habitats has piqued the curiosity of engineers and biologists for decades (Delf, 1932; Denny *et al.*, 1985; Gaylord *et al.*, 1994; Dayton *et al.*, 1999). Collaboration and interdisciplinary training between these groups of researchers have led to studies

Fig. 1. The biomechanical performance of macroalgae in moving water is driven by interactions between ambient flows, macroalgal forms, and the forces acting on and within the macroalgae. These components are also interdependent: flow and form influence the magnitude of forces on macroalgae, force and form influence the flow conditions via motion of the macroalgae, forces shape macroalgal forms through damage and plastic growth responses, and forms alter flows at small scales (ruffles can drive turbulent flow along the surface of a macroalgal blade) and at large scales (dense aggregations produce slow flow in the interiors of macroalgal canopies and fast flow along the outer edges of canopies).

of macroalgal biomechanics that employ quantitative analyses and comparisons of biomechanical traits (with principles of engineering) in ecological and/or evolutionary contexts (with principles of biology) (Denny *et al.*, 1985; Vincent and Gravell, 1986; Carrington, 1990; Koehl, 1999; Rosman *et al.*, 2013). Unfortunately, the physically challenging conditions that make macroalgal habitats biomechanically interesting often, but not always, prevent *in situ* examinations of macroalgal biomechanics—for instance, waves can damage delicate instrumentation and threaten the safety of investigators (Stevens *et al.*, 2002; Gaylord *et al.*, 2013). In response, many examinations remove the organisms from nature to study them under controlled conditions in laboratories or they estimate *in situ* biomechanical processes, such as bending and deformation in flow, using numerical or physical models (Vincent and Gravell, 1986; Friedland and Denny, 1995; Gaylord *et al.*, 2001; de Bettignies *et al.*, 2013a; Rosman *et al.*, 2013). These approaches also tend to select for or assume idealized forms of macroalgae (e.g. free of disease or damage) and simplified flow patterns that may not be truly representative of natural conditions (Huang *et al.*, 2011; Burnett and Koehl, 2019; Gutow *et al.*, 2020). Thus, while laboratory and modeling studies of macroalgal biomechanics enable investigations of controlled and simplified conditions, they do not necessarily capture all complexities of flows, forms, and forces that occur in nature. Field studies, on the other hand, can capture these complexities, but, because of their opportunistic nature, they do not necessarily span the full range of these variables neither are they as effective for precisely isolating the biomechanical consequences of individual variables.

Studies that get close to examining macroalgal biomechanics *in situ* tend to focus on catastrophic (maximal) biomechanical processes (i.e. tissue breakage, dislodgement) in which the morphology and survival of macroalgae can be measured safely before and after an extreme event (e.g. waves, storms) (Black, 1976; Demes *et al.*, 2013; de Bettignies *et al.*, 2013b; Burnett and Koehl, 2020). However, the actual process of mechanical failure is often not observed and the submaximal interactions between flows, forms, and forces are neglected. Submaximal interactions are an important component to the ecological performance of macroalgae because they comprise most of the interactions between macroalgae, flow, and forces (i.e. up to the point of failure). For instance, plastic changes in macroalgal form occur in response to submaximal interactions with flow and force, and, in some cases, repeated submaximal loading cycles (e.g. from waves) can lead to mechanical fatigue and failure of macroalgae (Mach, 2009; Coleman and Martone, 2020; Koehl and Silk, 2021). We therefore know little about the biomechanical performance—and especially the submaximal, biomechanical performance—of macroalgae over the course of their lives and under the full range of flows and forces that occur in nature.

Here, we review methods for measuring the flows, forms, and forces that are integral to understanding the biomechanical performance of macroalgae in nature. We describe
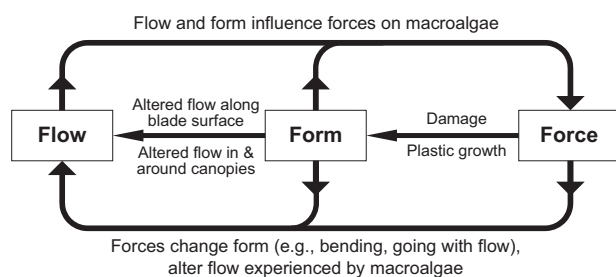
whether these methods are suitable and accessible for field use to examine macroalgal biomechanics under natural conditions. We discuss whether these methods provide mechanistic information about the submaximal and/or maximal biomechanical performances of the organisms. Finally, we review how flow, form, and force data can be integrated into frameworks to facilitate comparative studies of macroalgal biomechanics and to develop a comprehensive, mechanism-based understanding of the functional performance of macroalgae in challenging flow conditions.

Quantifying flow

Why is it important to quantify flow?

Water motion plays critical roles in the biology of macroalgae, and understanding these roles requires that fluid movement be quantified with relevant metrics and on relevant spatial and temporal scales. For instance, long-distance dispersal of macroalgal fragments and propagules depends on water motion over the course of days and kilometers, whereas shorter dispersal depends on water motion over the course of hours and meters (Gaylord *et al.*, 2006; Fraser *et al.*, 2020); diffusion of nutrients across the surface boundary layers of macroalgal blades—moving from the water column to the blade surfaces—depends on water motion over seconds and millimeters (Hurd *et al.*, 1996; Pujol *et al.*, 2019; Vettori and Nikora, 2019). Paradoxically, the rapid water motion that facilitates the diffusion of nutrients to the surfaces of macroalgae (benefiting their productivity) can also subject macroalgae to excessive hydrodynamic forces and serve as a source of mortality (if the macroalgae are dislodged) (Koehl and Wainwright, 1977; Hurd *et al.*, 1996). Because flow patterns can also change over space and time (e.g. between an offshore buoy and an onshore organism) due to interactions with the benthos or attenuation of wave energy, flow should be measured at a physical location that is relevant to the process under investigation (Seymour *et al.*, 1989; Gaylord, 1999; O'Donnell and Denny, 2008). In addition, the biomechanical interactions between macroalgae and flow can occur over a wide range of temporal scales, such that appropriate flow measurements are context dependent, for example an instantaneous mechanical response to flow versus a long-term growth response to flow (Coleman and Martone, 2020; Burnett and Koehl, 2021; Koehl and Silk, 2021). However, the biomechanical performance of a single component (e.g. structure, tissue) of a macroalga in flow frequently depends on the interactions of the entire organism with flow (Denny *et al.*, 1998). Therefore, appropriate measurements of water motion should occur at the scale of the organisms (or component of the organism), near the organisms (so flow measurements are representative of flow experienced by the macroalgae), and at a frequency and duration that match the rate and duration of the biomechanical process in question.

What flow patterns exist in macroalgal habitats?

Water motion in macroalgal habitats can be classified simplistically as unidirectional currents, wave-driven (oscillatory) flows, or a combination of the two (Seymour *et al.*, 1989; Johnson and Koehl, 1994; Gaylord, 1999, 2000; Gaylord *et al.*, 2003; Bekkby *et al.*, 2019). Despite these broad characterizations, the actual flow velocities that occur within macroalgal habitats can vary considerably across space and time. For instance, flow in currents can change with the timing of the tides, flow in waves can change rapidly over a single wave cycle, and flow in both settings can depend on season and the presence of storms (Johnson and Koehl, 1994; Gaylord, 1999). As waves break, they furthermore create fluid turbulence that is more difficult to characterize but may also be relevant (Gaylord, 2008; Gaylord *et al.*, 2013). For example, levels of turbulence influence exchange processes at blade surfaces, including processes tied to carbon uptake by macroalgae (Stevens *et al.*, 2003; Fram *et al.*, 2008), and can alter rates of delivery of macroalgal spores to the substratum following their release into the water column (Gaylord et al., 2002, 2004). Water motion is also altered by the form and arrangement of macroalgae: ruffles in the surfaces of blades can prompt turbulent mixing of flow near the blade (Hurd *et al.*, 1996), dense clusters of macroalgae reduce flow velocities within the aggregations (and speed up flow velocities along their outer edges), and individual macroalgae prompt turbulent mixing of water as it moves around their thalli (Gaylord et al., 2004, 2007; Rosman et al., 2010, 2013). Thus, the dominant flow regimes, along with nearby physical features that cause spatial and temporal augmentations of water motion, should be considered carefully when deciding how, where, and when water motion is measured for biomechanical investigations of macroalgae.

Quantifying wave properties

Often the dominant component of water motion acting on macroalgae is produced by waves. In such cases, flow in macroalgal habitats can be quantified or characterized with local wave data, which are available at many, but not all, sites around the world. Networks of buoys (e.g. www.ndbc.noaa.gov) can provide data for near- and offshore waves, such as dominant wave period and significant wave height (average height of the third largest waves over a certain window of time). Despite their nearly global extent, many remote sites are located far from a buoy or, conversely, some buoys may serve large geographic areas, which can obscure wave differences between sites. Coastal research stations often have dedicated wave sensors near their facilities that provide detailed, high-frequency measurements of wave conditions, and some research groups have designed do-it-yourself (DIY) sensors for characterizing near- and onshore wave data that provide the same types of information as commercially available wave sensors, but at a fraction of the cost. These varying approaches

rely on many of the same underlying sensors, including pressure sensors, accelerometers, and two-wire resistance gauges. Briefly, pressure sensors on the seafloor quantify the elevation of water above the sensor (Gaylord, 1999; Lyman *et al.*, 2020); accelerometers in tethered buoys at, or just below, the water's surface quantify the motion, and thus height, of ocean swells (Evans and Abdo, 2010; Figurski *et al.*, 2011; Yurovsky and Dulov, 2017; Focht and Shima, 2020); and two-wire resistance gauges at the air–water interface measure the elevation of the water's surface (Stevens *et al.*, 2002) (details on using these sensors are available within the referenced literature). A major benefit of these methods is that they are compatible with high-frequency data collection that can produce a profile of the wave environment over time, allowing calculations of the local wave climate. However, a negative aspect of these devices is that they are often prone to error when exposed to breaking waves: impact forces from waves can give erroneous pressure readings unrelated to the true water elevation; foaming air–water mixtures can short-circuit resistance gauges and give incorrect water elevation readings; and tangling of buoy tethers with macroalgae or other equipment can interfere with accelerometer readings (Gaylord, 1999; Stevens *et al.*, 2002). Although wave property data are readily available for many places around the world, we anticipate that advances in DIY technology will soon produce sensors that can (i) avoid erroneous measurements from breaking waves and (ii) be deployed along remote shorelines where data are currently unavailable, allowing direct measurements of wave properties within or close to macroalgal habitats.

At sites where wave conditions are monitored (e.g. from oceanographic observing platforms), data may not always be presented in the most accessible format for studies on macroalgal biomechanics. For instance, data may be available only as summary data that characterize sea state during a given time period, such as wave spectra, significant wave height, and dominant wave period (Kinsman, 1965). However, some advanced observing platforms record data about wave directionality and, if raw data from sensors can be accessed, other flow attributes can be determined—for instance, pressure changes associated with variation in the height of the overlying water column as waves propagate overhead, accelerations of the sea surface as it moves up and down due to passing waves (e.g. 'waverider' buoys), or fluid velocities produced by wave orbits throughout the water column (e.g. acoustic Doppler current profilers) (Gaylord and Denny, 1997; Emery and Thomson, 2001; Lyman *et al.*, 2020). Thus, the utility of wave summary data (spectra, heights, periods) for field studies of macroalgal biomechanics can be enhanced if more detailed time series data underlying the summary statistics are available. We expect that, in the future, observing platforms and DIY wave sensors will incorporate additional sensor types that further increase the relevance of their data for biomechanical investigations of macroalgae.

In some cases, wave data may not be the most useful information for understanding detailed aspects of flow in macroalgal habitats. For instance, if one is interested in biomechanical factors driving dislodgement and mortality in seaweeds, a crucial factor is likely to be the peak velocity produced by waves, which is related to wave length, height, and direction, and water depth. Linear wave theory (Denny, 1988) can be used to infer velocities from wave property data, but the techniques are not always straightforward, often require knowledge of spectral analysis (Gaylord and Denny, 1997; Morris *et al.*, 2019), and may be difficult to apply if the wave data originate from offshore sensors rather than ones placed at the local site of interest. Indeed, as waves propagate from deeper into shallower water, they change appreciably in height, may wrap around obstacles or refract to a new alignment, become focused onto a particular sector of shore, or interact with previous waves that have been reflected from the coast (Komar, 1976; Denny, 1988). Moreover, as waves reach the shore and overturn or collapse, and break to form the familiar 'whitewater' of the surf zone, their velocities become further complicated (Gaylord, 1999, 2008). Therefore, in these scenarios, direct measurements of water velocities, rather than estimations based on theory, may be preferable.

When wave data are limited and water velocities are not explicitly needed, researchers can use alternative classifications of local wave conditions, including wave fetch, wave run-up, and ranked wave exposures. Briefly, wave fetch refers to the offshore distance over which waves can build, with bigger fetch producing bigger waves (Burrows *et al.*, 2008; Burrows, 2012); wave run-up refers to the vertical distance on the shore that waves can reach, with bigger waves reaching farther up the shoreline (Schüttrumpf *et al.*, 2009); and ranked wave exposures rely on categorical definitions of wave sizes, which may be based on factors including the orientation of the shoreline and local biota—shorelines that directly face oncoming waves and that have smaller, sessile organisms tend to have bigger waves (Jones and Demetropoulos, 1968) (details on using these methods are available within the referenced literature). These approaches can broadly characterize waves on any coastline, but their applications are limited due to low spatial resolution (e.g. typically one classification per shoreline), they may not be easily comparable between sites, and they do not reveal temporal variation in wave properties. Although these wave classification methods have proven useful in many ecological studies of macroalgae, their low temporal and spatial resolution may make them unhelpful for most studies of macroalgal biomechanics.

Quantifying water velocities

Several methods exist to quantify water velocities in macroalgal habitats, including commercial and DIY sensors that span capabilities from single-point, single-dimension measurements to high-frequency, multidimensional measurements. In practice,

the best methodologies complement the speed, duration, and directionality of the biomechanical processes under investigation. For instance, assessing a long-term biomechanical trait in response to flow may require only the average or maximum water velocity for the sample period, whereas assessing a rapid biomechanical response (or a response to rapid fluctuations in flow) may require high-frequency sampling of water velocities; single-axis or directionless measurements may be appropriate when the axis of water motion is limited (e.g. in a channel), whereas multidirectional measurements may be appropriate when flow shows strong variation in multiple axes (e.g. during a wave).

Water velocities can be measured continuously, and with high-frequency and multidirectional data collection, using acoustic Doppler velocimeters (ADVs), acoustic Doppler current profilers (ADCPs), and drag sphere velocity probes (DSVPs): ADVs and ADCPs are typically only available commercially and are based on the Doppler shift effect, which is the change in frequency of a sound wave as it moves relative to a receiver or observer. ADVs measure relatively high-frequency flow velocities within a specific, small volume of water near the sensors (Voulgaris and Trowbridge, 1998); ADCPs measure velocity fluctuations within horizontal strata at given vertical positions in the water column, with newer models also providing data on wave conditions; and DSVPs are custom-built devices that measure the hydrodynamic forces acting on a sphere, which are then used to calculate flow velocities based on known relationships between water velocity and force on spheres (Donelan and Motycka, 1978). These devices can be mounted on the seafloor, but ADCPs can be deployed on vessels or buoys if coupled with positional data, and ADVs can be used as portable units with a lightweight scaffolding (Lohrmann *et al.*, 1995; Stewart, 2004; Boller and Carrington, 2006).

Water velocities can also be measured with devices that provide simpler characterizations of flow, typically with one measurement per deployment and only a single dimension: dynamometers use a spring scale with a drag element to mechanically record the largest hydrodynamic forces in a deployment, and the corresponding water velocity can be calculated from this force, as described above for DSVPs (Jones and Demetropoulos, 1968); clod cards, which are usually blocks or buttons of some dissolvable material, give a pseudo-quantitative measure of overall water motion based on the rate at which the clod card loses mass during a deployment (Gerard, 1982; Thompson and Glenn, 1994). These devices are inexpensive and simple to construct and deploy (Koehl and Alberte, 1988; Bell and Denny, 1994), but provide no directional data or information about higher frequency temporal variation.

In general, the benefit to these methods is that they can be used to directly measure flow velocities (with the exception of clod cards) rather than relying on theoretical or statistical relationships to infer flow velocities from wave summary statistics (Gaylord, 1999). These methods facilitate data collection within the habitat or next to the macroalgae being studied

(Gerard, 1982; Koehl and Alberte, 1988; Gaylord *et al.*, 2008). However, the instruments that provide high-frequency, multidirectional flow measurements may not be accessible due to the high cost of commercially available equipment (e.g. ADVs), the technical expertise needed to build DIY sensors (e.g. DSVPs), or the need to alter the shoreline to install equipment (e.g. drilling holes for mounting sensors). Simpler devices (i.e. dynamometers, clod cards) are generally more accessible but do not provide the same frequency or directionality of flow velocity measurements (Jones and Demetropoulos, 1968; Gerard, 1982; Bell and Denny, 1994; Thompson and Glenn, 1994). Therefore, *in situ* measurements of flow velocity, especially high-frequency flow measurements, are not widely available for many sites. We expect that future innovations with DIY velocity-measuring technology, as with recent innovations in wave-measuring technology, will make high-frequency, multidirectional flow measurements more accessible, enabling researchers to collect flow data in macroalgal habitats with the appropriate level of detail. An example outcome of this development is that analyses that were previously limited to dynamometer readings for maximum water velocity (in an unknown direction) over a multiday period could quantify water velocities in specific axes and at high frequencies. These new data could be used to test, or even fuel additional, hypotheses about the mechanical performance of macroalgae in nature.

Even if sensors are capable of high-frequency, multidirectional flow measurements, they may have finite power supply and data storage capacity, which creates a trade-off between total deployment time, sampling duration, and sampling frequency. For instance, continuous, high-frequency measurements can quickly exhaust the power supply and/or data storage, providing a relatively brief high-resolution snapshot of water motion experienced by macroalgae (Boller and Carrington, 2006). One solution is intermittent sampling, with bursts of high-frequency measurements (e.g. record for 1 min every 10 min), which reduces the duration of continuous sampling but extends the total deployment time (Stevens *et al.*, 2002; Gaylord et al., 2007, 2008). Intermittent sampling may provide data sufficient to quantify mean flow (compared with continuous, high-resolution sampling), but it may miss brief, anomalous events that elicit the maximal or near-maximal biomechanical performance of macroalgae. These power supply and data storage barriers will probably attenuate in the coming years with technological advances, leaving researchers with only the analytical challenge of interpreting vast amounts of flow data.

Within the technical and logistical constraints of flow measurement and data processing, increasing sample frequencies and directions provides an increasing amount of useful flow data for biomechanical studies of macroalgae. For instance, devices that measure flow in multiple directions (i.e. longitudinal x, lateral y, vertical z) with moderate or high sampling frequencies provide data that can be used to infer detailed flow–form interactions and temporal trajectories of force imposition on

macroalgae. In contrast, the simplest flow-measuring devices that make one measurement per deployment effectively collect summary data (i.e. aggregate water motion and maxima for clod cards and dynamometers, respectively), with one data point used to approximate broader flow characteristics (across some loosely defined range of x, y, and z). Sample frequency becomes increasingly important when describing strongly fluctuating flows. For instance, periodic oscillations in water velocity due to waves can be quantified, followed if desired by additional spectral analyses to identify dominant frequencies of the flow past macroalgae (Jackson and Winant, 1983; Gaylord *et al.*, 2007). In even more rapidly changing flows, such as those with appreciable accelerations (i.e. the first derivative of velocity with respect to time) (Gaylord, 1999) or stochasticity, fluctuations in water velocity can be represented in terms of the 'turbulence intensity' or 'turbulent kinetic energy', which characterize the higher frequency variance of water velocity over time (Leonard and Luther, 1995; Robinson *et al.*, 2013). Overall, water velocity measurements and the subsequent velocity-based calculations are ideally made with a level of detail that complements the speed, duration, and directionality of the biomechanical processes under investigation.

Attributes of flow data limit the detail of biomechanical analyses

Often, the accessibility of flow-measuring equipment is a driving force in deciding how flow is measured, influencing the detail with which macroalgae–flow interactions are examined. For instance, offshore measurements of wave properties (e.g. archived in publicly available databases) or tidal currents may be the most feasible way to estimate flow in shallower macroalgal habitats when direct measurements of flow velocities are not possible (e.g. due to logistical constraints, remoteness of field sites, or funding). However, estimating near- or onshore flow from offshore instruments may not provide the most accurate information about the flow experienced by macroalgae onshore, due to changes in wave properties that occur as waves shoal (Thornton and Guza, 1983), or changes in currents as they interact via frictional processes with the coast (Nickols et al., 2012, 2015). Similarly, techniques that record a single maximum or mean flow velocity per deployment may be accessible, but they fail to capture high-frequency variation in flow that can be crucial to understanding the biomechanical performance of macroalgae. In particular, the maximum flow velocity indicated by a dynamometer does not reveal how often or for how long the maximum flow velocity occurred, and an aggregate measure of fluid motion as indicated by a clod card does not reveal the frequency distribution or time course of flow velocities around the mean speed.

Due to the limited accessibility of equipment for making detailed measurements of water velocities in macroalgal habitats, *in situ* biomechanical investigations of macroalgae tend to focus on large-scale or population-level phenomena, such as

morphological comparisons between populations for which measurements of wave properties near each population provide an adequate assessment of relative flow conditions between populations (Blanchette, 1997; Blanchette *et al.*, 2002; Kitzes and Denny, 2005; Henkel *et al.*, 2007; Coppin *et al.*, 2020). Field studies have also focused on maximal water motion and maximal performance of macroalgae, such as using offshore wave data or onshore maximum velocities to infer extreme flow conditions and test whether macroalgal morphology is correlated with the organisms' survival through the challenging flow (Seymour *et al.*, 1989; Blanchette *et al.*, 2002; Demes *et al.*, 2013; Burnett and Koehl, 2020). Thus, broad, correlative studies of macroalgal biomechanics have prevailed over fine-scale, mechanistic studies in part due to the inaccessibility of flow-measuring equipment.

Recent innovations in flow-measuring technology, particularly DIY methods with off-the-shelf components, have made direct, high-frequency measurements of flow in macroalgal habitats more accessible. Although many DIY designs are currently tailored to measure flow in submerged macroalgal habitats without breaking waves, the coming years will probably bring designs that can record high-frequency measurements of flow in onshore macroalgal habitats with breaking waves. These devices will enable improved quantification of flow in macroalgal habitats with increased precision and frequency, which can then facilitate fine-scale, mechanistic studies of macroalgal biomechanics in nature.

Quantifying form

Why is quantifying form important?

Form is central to the biomechanical performance of macroalgae in moving water: the magnitude of hydrodynamic forces a macroalga experiences from moving water, as well as its biomechanical response to the forces (which can in turn further influence the imposed force, e.g. when a macroalga bends or flutters), are each influenced by the organism's form (Fig. 1). In this context, 'form' includes the size, shape, and orientation of a thallus, and the mechanical properties of its tissues and overall structure. These traits can each be considered static in terms of instantaneous interactions with flows and forces, or as dynamic traits that change in response to local flows and forces, and with growth of the macroalgae (Fig. 2). Quantifying static and dynamic forms is important because it can aid in evaluating both the submaximal and maximal performance of macroalgae in moving water: maximal performance (i.e. when macroalgae are damaged or dislodged) is generally described by comparing the distribution or presence of static forms before and after a mechanically challenging event in nature (Blanchette, 1997; Demes *et al.*, 2013; de Bettignies *et al.*, 2013b; Burnett and Koehl, 2020); submaximal performance is generally described by monitoring dynamic forms, such as thallus reconfiguration in response to increasing

water velocities in laboratory flumes where flow is highly controlled, or quantifying biomechanical performance (e.g. hydrodynamic forces) as a function of static form in laboratory flumes or field settings (Koehl and Alberte, 1988; Boller and Carrington, 2006, 2007; Gaylord *et al.*, 2008; Martone *et al.*, 2012; de Bettignies *et al.*, 2013a). Although laboratory flumes provide important information about static and dynamic forms in response to controlled flow conditions, they may not always elicit the same form responses to the complex flow conditions that can occur in nature (e.g. entire thalli swaying back and forth in waves while individual blades flutter in the passing flow). Moreover, variation in the design of flumes, and the resulting differences in flow regimes and velocities, may interact differently with various morphologies of macroalgae (Martone *et al.*, 2012). Luckily, measuring geometric aspects of form, such as size, shape, and orientation, relies largely on photographic techniques that are widely accessible due to the low cost of cameras and the availability of software for analyzing photographic data. Therefore, there are many opportunities to apply laboratory-based techniques for measuring

macroalgal form to field studies; however, to understand the role of form in macroalgal biomechanics, we must take care to measure these traits in ways that match the biomechanical processes under investigation.

Size, shape, and orientation

Macroalgal size can be measured through video or photographic techniques that are suitable for use in the field and laboratory (Fig. 2). Planform (or Plan) Area is the area of the thallus visible from above when laid on a flat surface. Natural overlap or clumping of thallus tissues will typically make the Planform Area less than the Total Thallus Area, which is the combined area of all thallus structures, measured individually. Projected (or Frontal) Area is the cross-sectional area of a thallus facing flow. While Planform Area and Total Thallus Area can be measured out of the water (on either unaltered or harvested specimens) and are measurements of a static form, Projected Area requires a camera to be in-line with the thallus (either upstream or downstream) while it is experiencing
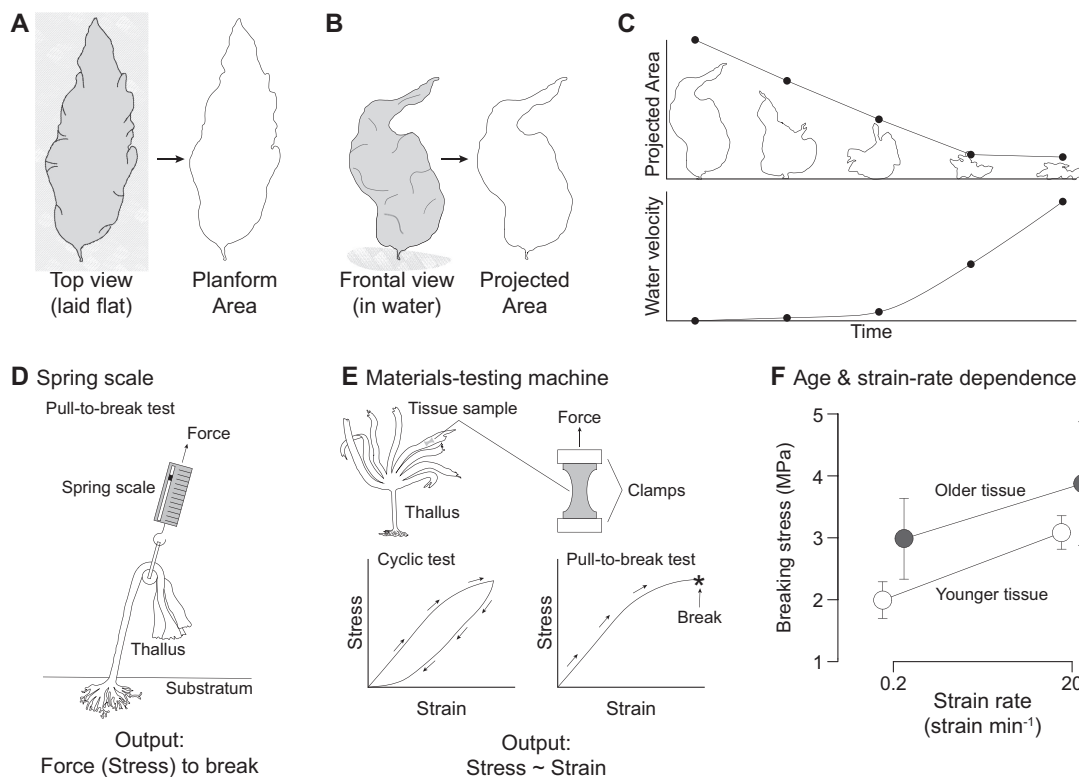

Fig. 2. Common methods for quantifying macroalgal form. Whole thallus morphology can be described by (A) Planform Area, which is typically a static feature measured when the thallus is laid flat out of the water, and (B) Projected Area, which is the thallus area facing flow. Projected Area can be treated as a static form if measured at a single water velocity or (C) as a dynamic form if measured over time in fluctuating flow. Mechanical properties of macroalgal tissues can be measured (D) in the field using spring scales for pull-to-break tests on whole thalli or (E) in the laboratory using a materials-testing machine with tissue samples. Materials-testing machines can conduct cyclic tests or pull-to-break tests of the tissue. (F) Tissue age (often related to position on a thallus) and strain rate (change in sample length per time divided by initial sample length) may affect the mechanical properties of macroalgal tissues, and these factors can be controlled using materials-testing machines. Images in (A–C) are based on Martone *et al.* (2012) and Krumhansl *et al.* (2015), with permission. Image in (E) is based on Teagle *et al.* (2017), with permission from Elsevier. Data in (F) are from Burnett and Koehl (2021), with points and error bars showing means and SDs, respectively.

water motion and can be measured as a dynamic form (e.g. it is monitored as flow fluctuates) (Martone *et al.*, 2012). In the field, this requires a camera submerged with the macroalgae, while in the laboratory this can be accomplished with a camera outside of a flume that has transparent walls. It is possible for each of these aspects of size to be measured non-destructively in the field using photographic methods, and we expect that many field investigations of macroalgal biomechanics in the future will use these methods to quantify thallus size without altering the test subject.

Moving beyond size, a versatile metric for shape is the Flatness Index (FI), calculated as (Planform Area)$^{3/2}$ divided by thallus volume (Gaylord, 2000; Gaylord *et al.*, 2008; de Bettignies *et al.*, 2013a). Thallus volume is found by dividing the thallus weight by the density of macroalgal tissue, which studies show can range from at least 840 kg m^{-3} to 1486 kg m^{-3} (Gaylord, 2000; Paul *et al.*, 2014; Vettori and Nikora, 2017), or via water displacement techniques (Stewart and Carpenter, 2003). FI describes how three-dimensional the thallus is compared with a flat sheet, where FI=1 is a perfectly flat thallus and FI>1 is a 'clumped' thallus. It has typically been used as a static form but could also be measured as a dynamic form if Planform Area and thallus volume were monitored over time (i.e. as a macroalga grows). In contrast to methods for determining size, FI determination usually requires destructively weighing the thallus (i.e. removing it from the substratum), although many macroalgal species can survive (at least temporarily) removal from and re-attachment to the substratum (Blanchette *et al.*, 2002; Stevens *et al.*, 2002). Establishing FI as a common and standardized way to quantify macroalgal shape (and its variation over time) *in situ* can encourage future studies that examine how shape and other traits influence the biomechanical performance of macroalgae during short-term (e.g. instantaneous) and long-term (e.g. with growth) interactions with moving water.

Thallus orientation in the water column is a dynamic form that gives context to other biomechanical measurements, for example which way was the thallus facing when it was impacted by a wave? Thallus orientation can be quantified with video or photography, although the camera's field of view must match the range of motion of the thallus while also minimizing distortion due to parallax. This technique has been used in narrow, wave-swept surge channels where the motion and orientation of macroalgae were mostly limited to one dimension and were adequately captured by a single camera above the water, with a top-down view (Burnett and Koehl, 2017). Similar approaches have been used to quantify motion of terrestrial plants (Bian *et al.*, 2016; Kothari and Burnett, 2017; Zhang *et al.*, 2020). Capturing multiple dimensions of thallus orientation is possible with multiple camera views and software for reconstructing three-dimensional spaces from multiple two-dimensional images (Katija and Dabiri, 2008; Hedrick, 2008). Hedrick (2008) also includes tutorials for extracting positional data from videos that are helpful to new users. To our knowledge, video analyses (two- or three-dimensional) of thallus orientation in the field are not a widespread technique in macroalgal biomechanics, but we expect that the method's feasibility with helpful software tutorials and the increasing affordability of field-portable cameras will make this approach more common. Consequently, field studies of macroalgae will be more powerful because the thallus orientation and positional data from videos will give greater context to the measurements of biomechanical traits.

Thallus orientation has also been described using three-axis accelerometers attached to blade tissue; for example, signals can be integrated twice to give the position of the blade or classifications of signals can reveal unique modes of thallus reorientation in moving water (Stevens *et al.*, 2002; Harder *et al.*, 2006b; Mullarney and Pilditch, 2017). However, accelerometers alone may not always provide reliable or useful data because they can detect accelerations from several aspects of macroalgal motion (e.g. turning to move with ambient flow, fluttering vertically and horizontally) along with a signal from gravitational acceleration that may appear on any one of the sensors' axes as the macroalgae rotate (flip upside-down, turn) and move in the flow. In these cases, it is prohibitively difficult to distinguish accelerations due to the macroalgae's motion from accelerations due to the shifting gravitational signal. Future integration of accelerometers with other means of tracking orientation (e.g. video, gyroscopes) may give more context to the data from accelerometers and bolster their use within biomechanical analyses.

Mechanical properties

Mechanical properties of macroalgal tissues can be measured with techniques that assess whole thallus structure or that examine excised tissues from specific thallus regions (Fig. 2). A common field technique uses a spring scale to pull on a thallus, whole or in part, to measure the maximal force the thallus can resist (Black, 1976; Carrington, 1990; Blanchette *et al.*, 2002; Martone *et al.*, 2012). The breaking force is recorded by the spring scale and can be described as a tissue-specific material property (i.e. tensile strength) by dividing the force by the measured tissue's cross-sectional area (Niklas, 1992). As this technique is limited to the breaking force of the thallus, it only provides information about the maximal performance of macroalgae.

In the laboratory, mechanical properties of tissues can be measured with materials-testing machines (e.g. Instron) that require excised tissues from the thalli (or thallus structures that can naturally fit within the machines). With these devices, tissue samples can be stretched ('strained') at specific rates and the resulting stress in the tissue can be measured at a high frequency (e.g. 10 Hz). Materials-testing machines can often be programmed to evaluate the mechanical properties of the sample under submaximal stress and strain levels (e.g. cyclic loading) or maximal levels (e.g. pull-to-break tests; Fig. 2) (Koehl and Wainwright, 1977; Johnson and Koehl, 1994; Denny *et al.*, 2013; Denny and King, 2016). When

commercially available materials-testing machines are prohibitively expensive, other methods are available: tissue samples can be clamped at each end, as with a materials-testing machine, with one end attached to a stationary platform and the free end attached to a vessel, and forces (e.g. weights) can be added to the vessel at a known rate while the sample's deformation is recorded (Simonson *et al.*, 2015; Sirison and Burnett, 2020). Material properties can also be quantified using a variety of static loading configurations with either concentrated or distributed loads (Roark *et al.*, 2020), such as three-point bending arrangements and cantilever arrangements (Harder *et al.*, 2006a; Henry, 2014; Vettori *et al.*, 2020). Details of the necessary formulae and their implementation are available in the referenced literature. Overall, these methods provide more detailed information than pull-to-break tests with spring scales, but they come at the small cost of reduced throughput because many samples need to be brought into the laboratory and prepared (excised, cut into a working section) rather than tested directly in the field as with spring scales.

Recent studies of the mechanical properties of macroalgal tissues with materials-testing machines revealed that many methodological details can affect the observed mechanical properties. For instance, strength and stiffness of macroalgal tissue can increase with the tissue's age (Krumhansl *et al.*, 2015; Burnett and Koehl, 2019), but field measurements with spring scales are not always able to control for the age of the measured tissue (e.g. the thallus is pulled until it breaks, and the age of the tissue where the breakage occurred is not considered or controlled). In addition, mechanical properties of macroalgal tissues can depend on the rate at which they are strained (Burnett and Koehl, 2021), but field measurements with spring scales cannot precisely control how rapidly or slowly the thallus is pulled by the experimenter. Thus, differences in mechanical properties of tissues may be obscured if a field spring scale method is used versus a laboratory materials-testing machine. Also, whether measured by materials-testing machines in laboratories or by spring scales in the field, mechanical properties of macroalgal tissues are often considered to be static traits. However, age and strain rate dependencies of mechanical properties in macroalgal tissues indicate that they are in fact dynamic traits (Fig. 2). Therefore, future studies should consider the extent to which the tissues of their model systems exhibit mechanical properties that depend on the time scale of force application and, if necessary, measure mechanical properties with techniques that match the physical (e.g. strain and loading rate) and biological (e.g. tissue age) conditions of the biomechanical processes that occur in nature.

Quantifying forces (and stresses/strains in tissues)

Why is it important to quantify forces?

Macroalgal tissues are routinely loaded by physical forces from the environment, including forces from water motion, buoyancy, inertia, and mechanical interactions with nearby structures: water motion relative to macroalgae produces hydrodynamic forces—detailed descriptions and derivations of these forces are available elsewhere (Denny, 1988; Vogel, 1996); buoyancy of the macroalgae produces a tensile force pulling the macroalgae towards the water's surface (Stewart, 2006; Burnett and Koehl, 2017); rapid deceleration ('jerking' to a halt) after passively moving with the ambient flow produces an inertial force on macroalgae (Gaylord and Denny, 1997; Denny *et al.*, 1998; Gaylord *et al.*, 2008); and mechanical interactions from macroalgae tangling, scouring, or impacting other structures produces tensile, compressive, and shearing forces within the organisms (Koehl and Wainwright, 1977; Kennelly, 1989; Hughes, 2010; Burnett and Koehl, 2018). These forces all manifest as mechanical stresses and strains within macroalgal tissues. If the magnitudes of either the stresses or strains in the tissues exceed the tissues' maximum strength or extensibility, the affected tissues can break from the macroalgae, which may result in the loss of the entire thallus if the stipe, holdfast, or other support tissues are compromised (Denny *et al.*, 1989; Burnett and Koehl, 2019). Excessive sublethal breakage of tissues (i.e. those not involved in supporting a thallus) can decrease the growth and survival of the macroalgae and ultimately lead to mortality (Burnett and Koehl, 2020). In contrast, submaximal stresses and strains can prompt plastic growth or repair responses from macroalgae, altering their morphology and subsequent interactions with agents that exert loads on the macroalgae (Coleman and Martone, 2020; Koehl and Silk, 2021). Thus, quantifying the mechanical forces exerted on macroalgae is important because they shape the growth, damage, performance, and survival of macroalgae in their physically challenging habitats.

Quantifying forces on macroalgae

In contrast to the numerous methods for quantifying water motion, there are limited options for directly measuring the forces on macroalgae in field settings. Two devices used in recent years are multi-axis force plates and single-axis load cells (Gaylord, 2000; Stevens *et al.*, 2002; Boller and Carrington, 2006; Gaylord *et al.*, 2008) (Fig. 3). Both force-measuring devices can sample at high frequencies and for long durations if data storage and power supplies allow (details on constructing and implementing these techniques are provided in the referenced literature). In practice, these devices have been used in brief deployments (e.g. 10 min) repeated at multiple points over several tidal cycles, with the aim to test theoretical models that relate macroalgal morphology and instantaneous flow conditions to the instantaneous forces on the macroalgae (Stevens *et al.*, 2002; Boller and Carrington, 2006; Gaylord *et al.*, 2008). The goals of these studies have typically been to describe the factors influencing forces on macroalgae but not whether the forces exceed the mechanical limits of macroalgal tissues. Thus, these studies have focused

only on the submaximal forces experienced by macroalgae (i.e. they did not record the forces resulting in the damage or dislodgement of macroalgae). Recording forces that exceed the mechanical limits of macroalgal tissues requires long continuous deployments, which may not be possible with the current technology due to the required manipulation of the macroalgae (e.g. mounting to force plate, severing the stipes) that could lead to mortality or altered biomechanical behavior, along with other technical limitations (e.g. tangling of wires, limited data storage) (Gaylord, 1999; Stevens *et al.*, 2002). In the future, longer continuous deployments could be used to quantify how forces on macroalgae change over time with the general growth of the organisms and their plastic morphological responses to mechanical loads. Although the current technology permits detailed investigation of the instantaneous forces experienced by macroalgae, more developments to these tools are needed (i.e. less destructive to the macroalgae, longer deployment times) before they can be used to describe the long-term role of submaximal and maximal forces on the biomechanical performance of macroalgae.

Quantifying stresses and strains

Force plates and load cells only reveal the mechanical stresses experienced by the tissues adjacent to the sensor, not the tissues distal to the sensor (e.g. blades) (Fig. 3). Therefore, our empirical knowledge about the mechanical stresses that macroalgal tissues experience in nature is limited to tissue at the base or middle of stipes. We do not know the magnitude or distribution

of stresses at other parts of macroalgae, or how stresses vary over time as macroalgae are impacted by water motion, yet the stresses throughout the thalli of macroalgae are known to be important to their development (i.e. plastic growth in response to local stresses) (Koehl *et al.*, 2008; Coleman and Martone, 2020; Koehl and Silk, 2021). For example, macroalgae also lose and regrow more distal tissues in response to seasonal variation in hydrodynamic forces (i.e. they perennate, losing portions of their thalli to tattering but then re-expanding from a longer lived holdfast) (Gaylord *et al.*, 1994; Blanchette, 1997). Similarly, we know little about the local strains (stretching in response to a force) that macroalgae experience throughout their thalli in nature. Measuring these variables directly (e.g. finding where on a stress–strain curve, Fig. 2E, an organism falls) will provide information that is otherwise only available through extrapolation of material property data and measures of fluid flow. Thus, expanding our knowledge about the biomechanical performance of macroalgae in moving water requires an understanding of the stresses and strains that are experienced throughout their thalli.

There are currently no practical ways to measure naturally occurring mechanical stresses in the distal tissues of macroalgal thalli, but there are options for measuring strains, including sonomicrometry, Hall effect sensors, and video analysis—these techniques have typically been employed in the laboratory with macroalgae or in nature with other model systems. Recent successful applications of electronic devices for *in situ* studies of marine habitats suggest that these methods, with some modification, can provide new insights into the strains experienced by macroalgae in nature
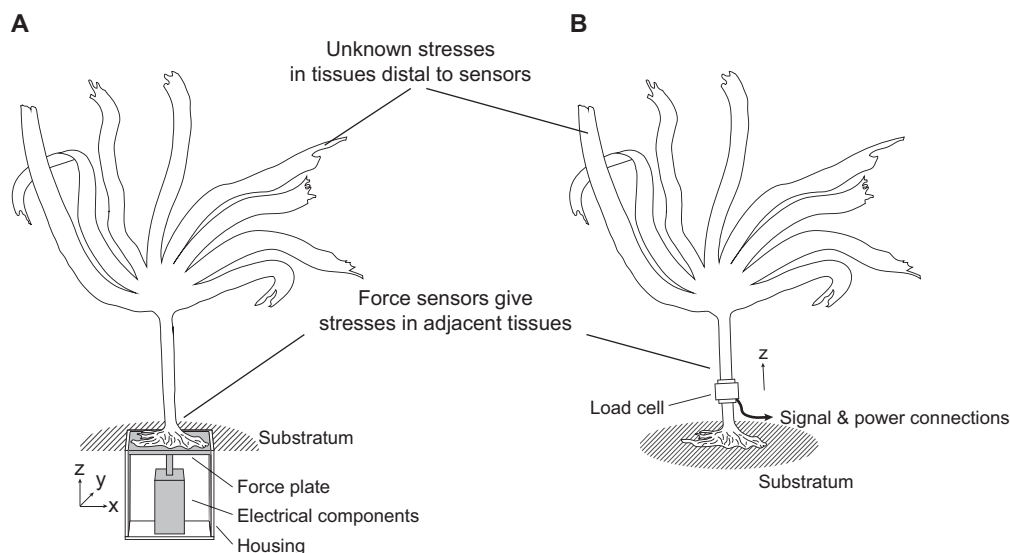

Fig. 3. Sensors for measuring forces on macroalgae. (A) Multi-axis force plates are mounted in the substratum with the holdfast of the focal macroalga attached to the plate in a realistic orientation and record forces in up to three axes. The electrical components of the force plate can include an internal power supply and data storage, or connections to external power supplies and data storage. (B) Single-axis load cells are spliced in line with the stipe to measure forces in the longitudinal axis of the stipe, and the sensor has connections to external data storage and power supply. Both styles of sensors only reveal the mechanical stresses in the tissue adjacent to the sensor. Illustrations are adapted from Gaylord (1999), Stevens *et al.* (2002), Boller and Carrington (2006), and Teagle *et al.* (2017), with permission from Elsevier.

(Lima and Wethey, 2009; Miller and Dowd, 2017; Lyman *et al.*, 2020). Sonomicrometry quantifies the distance between two piezoelectric crystals based on the time to send an acoustic signal between the crystals, and although it is traditionally used in carefully controlled laboratory experiments with animals (Sanford and Wainwright, 2002), this technique has been used to measure strains in macroalgae under laboratory settings (Hale, 2001). The crystals can be secured externally or internally to the tissue, but each crystal must be connected to a power source and data acquisition unit via wires, which may alter or be damaged by the normal mechanics of the macroalgae. Instructions for using this method in the laboratory with macroalgae have been described Hale (2001). Similarly, Hall effect sensors measure the distance between the sensor and a magnet (both attached to the organism), but, unlike sonomicrometry, only the sensor needs to be connected to a power supply and data acquisition unit. This technique has been used with bivalve molluscs in the field (Dowd and Somero, 2013; Miller and Dowd, 2017) but, to our knowledge, has not been applied to macroalgae. Instructions for using this technology are provided within the referenced literature. As with sonomicrometry, one downside of this approach is that the wires connecting to the sensor may alter or be damaged by the normal mechanics of the macroalgae.

Video analysis may be a useful option for quantifying strain in macroalgal tissues in nature because it is non-invasive and is commonly used to quantify structural deformations in other systems (Meresman and Ribak, 2017; Bhosale *et al.*, 2020; Cheng and Sun, 2021). Views from multiple cameras can also be combined to provide a fully parameterized three-dimensional space, with a large depth of field to keep objects in focus, in which strains can be quantified (Hedrick, 2008; Corcoran and Hedrick, 2019). Hedrick (2008) provides detailed instructions for obtaining three-dimensional camera views, along with a helpful graphical user interface that can facilitate (sometimes automatically, depending on video quality) the tracking of objects in videos. Video analysis does face considerable challenges. For instance, there may not be enough ambient light to detect natural landmarks on the macroalgae, in which case fluorescent markers or alternative light sources should be used (Delcourt *et al.*, 2011); larger macroalgae whose range of motion exceeds the field of view of the cameras may occasionally obscure the cameras' views of the targeted tissue; the resolution of strain measurements may scale with the size of the macroalgae and how close the cameras can be positioned (e.g. strain may need to be measured over a 50 cm section of a large thallus but only a 5 mm section of a small thallus). These methods may not provide continuous strain measurements, but they can provide brief glimpses of strain experienced by macroalgae in the field, which is biomechanical information that we do not currently have. Furthermore, these methods may be occasionally limited in resolution, but they should still be able to detect strain that approaches the maximum extensibility of the tissues, which can be an extension of >15% in length (Koehl and Wainwright, 1977). Because strains can be linked to stresses through the elastic moduli of a tissue (Koehl and Wainwright, 1977; Vincent, 2012), these tools can ultimately provide information about the mechanical stresses occurring in macroalgal tissues under field conditions, with the qualifier that moduli of biological materials are usually strain rate dependent, making the translation from strain to stress more challenging.

Future directions for force measurements

The devices described here for measuring forces on macroalgal holdfasts and stipes exist as custom-built equipment with no commercially available alternative, although researchers without the technical expertise to build the devices themselves can probably contract an outside party for construction. Notably, these devices have not been widely used within the last decade (Gaylord *et al.*, 2008) so there is great potential to update their designs with modern technology. Similarly, there is potential for adapting strain-measuring equipment (described above) to measure strains within macroalgae in nature due to the equipment's low cost and widespread use in other systems. To our knowledge, stress sensors that are suitable for use in the blade tissues of macroalgae in nature and that do not interfere with the mechanics of the tissue have yet to be created. Developing these tools, with an additional focus on long-term deployments, can enhance our knowledge of the magnitude, distribution, and sources of stresses, along with the macroalgae's biomechanical response to the stresses.

Frameworks for integrating flow, form, and force

Integrative frameworks that encompass flow, form, and force are helpful for describing specific features of macroalgae's biomechanical performance in moving water and for comparing macroalgal biomechanics between species and flow conditions, among other sources of variation. The frameworks described here have typically arisen from engineering-centric studies using numerical experiments and physical models (e.g. idealized forms, simplified flows) or from biology-centric studies using real organisms in laboratory settings (e.g. simplified flows); they have not been heavily applied to macroalgae in nature and therefore represent an opportunity to test lab- and theory-derived hypotheses of macroalgal biomechanics in field settings. Because the bases of these frameworks are detailed elsewhere, we limit our discussion to brief introductions and descriptions of how the frameworks may be applied to field studies of macroalgal biomechanics.

Passive reconfiguration in flow

The magnitude of drag (F_d), the hydrodynamic force acting parallel to the direction of flow, on a rigid object can be calculated as

$$F_d = \frac{1}{2}\rho A C_d u^2 \tag{1}$$

where ρ is fluid density, A is some reference area of the object, C_d is a non-dimensional drag coefficient describing the shape of the object, and u is fluid velocity relative to the object (Vogel, 1996). In studies of macroalgae, A is usually Planform Area, whereas in applications with bluff bodies, and across physics more broadly, A is often Projected Area. Consequently, the value of C_d will depend on which form of A is used, so care must be taken when comparing the implementation of Equation 1 across studies. As u increases, F_d for macroalgae generally increases at a lower rate than what is predicted by Equation 1 due to the ability of macroalgae to flexibly move with the ambient flow and reconfigure into streamlined shapes (Koehl, 1999). This movement, which we term passive reconfiguration because it occurs under the force of water motion without any active input from the macroalgae, is one biomechanical strategy that allows macroalgae to survive rapid water motion in their habitats.

Generally, reconfiguration of macroalgae can be quantified by statistically fitting measurements of F_d, u, ρ, and A into a re-arranged drag equation to estimate the remaining parameters, where the parameters themselves (or changes in the parameters as a function of u) describe reconfiguration. A potential downside to this method is that it ignores the brief forces that can arise from fluid acceleration, but it is still considered reliable because drag is, on average, the dominant force experienced by macroalgae (Gaylord, 2000; Gaylord et al., 2008).

The first of these reconfiguration frameworks captures how C_d changes as a function of u using a rearrangement of Equation 1:

$$C_d = \frac{2\,F_d}{\rho A u^2} \tag{2}$$

where decreases in C_d indicate an increase in streamlining (Vogel, 1989). Usually in these equations, A is considered independent of fluid velocity (Vogel, 1984), especially since most studies in this discipline use Planform Area, which is often treated as a static trait for macroalgae within the context of a short-term study (i.e. Planform Area can change with growth). However, instantaneous measures of A as Projected Area can be inserted into Equation 2 if the macroalgae are photographed while flow and forces are measured (Martone et al., 2012), with the caveat that the C_d calculated with Planform Area is not equivalent to the C_d calculated with Projected Area. In this context, the relative contributions of size (A) and shape (C_d) to the total reconfiguration can be extracted—changes in A and C_d compared between two water velocities.

The second reconfiguration framework considers the velocity exponent in Equation 1. This exponent is equal to 2 for rigid objects, but Vogel (1984) showed that other values of this exponent are needed to calculate drag on objects whose forms reconfigure in flow. Thus, Equation 1 can be re-written as

$$F_d = \frac{1}{2}\rho A S_d u^\gamma \tag{3}$$

where S_d is a shape term and γ is the velocity exponent (Gaylord et al., 2008). We use S_d here to distinguish it as a velocity-independent shape term, whereas C_d (from Equation 1) varies with velocity. The area term A is also velocity independent so that γ accounts for all reconfiguration within the measured range of u. We should note that elsewhere γ is presented as $2+E$, where E is a correction factor (the 'Vogel exponent') (Gosselin, 2019), but we use γ here for simplicity. Both S_d and γ can be estimated by statistically fitting F_d, u, ρ, and A measurements to Equation 3. For examples, see tables of S_d and γ reported by Gaylord et al. (2008) and tables of E reported by Vogel (1984) and Gaylord et al. (1994). This approach generally holds for the narrow range of u experienced by macroalgae, although studies of flat plates in flow suggest that γ can vary across large ranges of u as different regimes of reconfiguration occur (Gosselin, 2019). As a result, biomechanical studies of macroalgae across wide ranges of u may be better suited by quantifying reconfiguration with Equation 2 rather than Equation 3 because the shape term in Equation 2 can be calculated for discrete values of u (versus statistically fit to a distribution of u) and is not assumed to be independent of velocity.

Dynamic scaling of thallus motion in flow

Reconfiguration describes the passive streamlining response of macroalgae in flow, but thalli can also passively respond to flow by changing their orientation (i.e. going with the flow) and fluttering (Koehl and Alberte, 1988; Denny et al., 1998; Koehl, 1999). Here we present dimensionless quantities that describe the large-scale excursions of macroalgae in wave-driven flow and the fluttering motion of macroalgae in unidirectional currents.

In wave-driven flows, the motion of macroalgae relative to the ambient water motion within a wave cycle can be quantified as

$$L = \frac{D_{thallus}}{D_{wave}} \tag{4}$$

where $D_{thallus}$ is the distance traveled by some point on the thallus and D_{wave} is the distance traveled by the surrounding water (i.e. the integral of water velocity). This framework is based on a model by Luhar and Nepf (2016) that considered water motion (i.e. distance traveled) relative to thallus length. While the original model is valid, our modification allows for

L to be calculated across a wider range of macroalgal forms and flow regimes than are considered in the initial framework, which is necessary for this framework to be applied to more diverse and complex systems (e.g. species, flow regimes, or time scales). For instance, thalli may not return to the same 'starting position' at the end of one wave cycle, so the distance that the subsequent wave pushes them is not strictly determined by their thalli lengths. With video monitoring of thallus position, facilitated by automatic video tracking methods common to many other fields of biology (e.g. Hedrick, 2008), and field measurements of water velocity, *L* can be calculated over various sample periods (describing the average flow–form interaction) or instantaneously for full (or partial) wave cycles. When *L*<<1, water travels much farther than the thalli so the macroalgae are experiencing conditions close to unidirectional currents for most of each wave. When *L* is close to 1, the thalli are moving nearly as far as the water in each wave, experiencing values of *u* that are much less than the free stream velocities (i.e. *u* equals free stream velocity minus thallus velocity), and the macroalgae show little to no resistance (via stiffness, inertia, or buoyancy) to moving with the flow (Luhar and Nepf, 2016). Future applications of Equation 4 could pair *L* with F_d and *u* (Equations 1–3) to determine, for instance, at what point during a wave cycle a thallus reorients and moves with the ambient flow versus reconfigures its blades into a streamlined bundle (or both), and whether peak F_d are reduced for macroalgae when *L* falls in a certain range.

In unidirectional currents, the flapping of macroalgae can be analyzed by calculating the flapping Strouhal number (*St*) as typically applied to animal locomotion:

$$St = \frac{fl}{u}$$ (5)

where *f* is flapping frequency and *l* is flapping amplitude. *St* is frequently calculated for vortex shedding patterns, but is generally applicable to all oscillatory systems (Alexander, 2006), including the passive flapping of flexible objects in flow (Shelley *et al.*, 2005; Connell and Yue, 2007). Values for *f* and *l* can be measured in the field using video recordings in either two or three dimensions (Hedrick, 2008). Flapping can co-occur with the passive reconfiguration of flexible structures in flow and there is also a general pattern in which drag increases with flapping amplitude (Koehl and Alberte, 1988; Vogel, 1989). Future applications of Equation 5 alongside studies of passive reconfiguration (Equations 1–3) could reveal what aspects of flapping (or ranges of *St*) are most likely to disrupt reconfiguration and increase F_d on macroalgae.

Environmental stress factor

A key biomechanical trait for the survival of macroalgae is having the material strength to withstand the hydrodynamic forces of their habitats. Hydrodynamic forces experienced by macroalgae can vary between habitats and species, so

directly comparing the material strengths of macroalgae can be misleading without context. We can normalize the strength of a macroalga to the flow in its habitat by calculating its Environmental Stress Factor (ESF):

$$ESF = \frac{Breaking\ stress\ during\ life\ stage}{Peak\ stress\ experienced\ during\ life\ stage}$$ (6)

ESF shows how well suited the tissues of macroalgae are compared with the peak stresses (force per cross-sectional area) that are likely to occur during that life stage (Johnson and Koehl, 1994). Necessary data for calculating the ESF can be collected with *in situ* force measurements to calculate the peak stresses that can occur in nature, followed by breaking stress measurements. Alternatively, peak stresses can be estimated using Equations 1 and 3 with flow measurements from the field and form measurements of each macroalga, or part of a macroalga (i.e. calculating expected drag, and subsequently the drag per cross-sectional area of the thallus). This latter approach is not ideal compared with direct measurements because it reduces the complex morphology of a macroalga to a simple number based on a statistical relationship. The ESF has not been widely implemented in biomechanical studies of macroalgae, but existing data suggest that macroalgae can be >10 times stronger than the stresses they experience in peak growing seasons (i.e. spring and summer) (Johnson and Koehl, 1994; Sirison and Burnett, 2020). However, the ESF can decrease for macroalgae following reproduction or at the end of the major growing seasons (Johnson and Koehl, 1994). Future applications of Equation 6 could identify the relative roles of mechanical strength (the breaking stress) and morphology (influencing the peak stress) in the survival of macroalgae in moving water and whether these roles depend on factors such as flow habitat, life stage, and species.

Conclusions

Flow, form, and force are integral parts of the biomechanical performance of macroalgae in moving water. Testing hypotheses of macroalgal biomechanics in nature therefore requires adequate techniques for measuring these variables in the field. We reviewed methods and technology for quantifying flow, form, and force in nature and identified opportunities for improving the design and accessibility of these methodologies, and for adapting techniques from other study systems. For instance, flow sensors are becoming more available for many sites around the world due to advances in DIY technology, form-measuring techniques are largely lab based but are transferable to field settings, and force sensors exist as custom-built devices with decades-old designs that can be improved with modern components. We note that these methods often target either the maximal or submaximal performance of macroalgae, but both perspectives are needed to understand the biomechanics of these organisms over their lifetimes. Furthermore, data

should be collected on temporal and spatial scales that match the biomechanical phenomena being examined, but this is often limited by the capabilities of available technology. Finally, we describe several integrative frameworks (incorporating flow, form, and force) that can facilitate comparisons of macroalgal biomechanics in nature to predictions from theory and lab-based experiments. These frameworks, through their dimensionless outputs, can also be used to compare the biomechanical performance of macroalgae in moving water between different flows, forms, and force conditions. Applying these methods and frameworks to field settings can allow us to test many hypotheses of macroalgal biomechanics under the full range of natural conditions faced by these organisms, furthering our understanding of how macroalgae survive in such physically challenging habitats.

Author contributions

NPB conceptualized the topic, wrote the original draft, and was responsible for visualization; BG supervised the project. Both authors reviewed and edited the manuscript.

Conflict of interest

The authors declare that there are no conflicts of interest.

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