Hydrodynamic consequences of flexural stiffness and buoyancy for seaweeds: a study using physical models

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Summary

An upright posture in the water column may expose benthic marine organisms to faster flow higher in the water column than near the substratum, potentially increasing rates of mass exchange while also exposing the organisms to higher hydrodynamic forces. Benthic organisms maintain upright postures in the water column by one of two mechanisms, stiffness or buoyancy. *Turbinaria ornata* is a tropical macroalga that uses either buoyancy or flexural stiffness (*EI*), depending on its flow habitat. This study used physical models of *T. ornata* to compare the effect of different magnitudes of these two mechanisms on relative water velocity and hydrodynamic forces in both unidirectional and wavy flow. Models of the alga were constructed to span and exceed natural levels of *T. ornata*'s *EI* and buoyancy. Models with high *EI* and high buoyancy maintained upright postures in both unidirectional flow and waves, and experienced higher forces than models with low *EI* and moderate or low buoyancy that deflected in the direction of water motion. In waves, buoyant models that were deflected by high velocity rebounded back into upright positions when the flow slowed. Non-buoyant, flexible models were also pushed over by flow but lacked the ability to rebound upright, which led to decreased force in unidirectional flow, but high force in waves.

Key words: flexural stiffness, buoyancy, seaweed, *Turbinaria ornate*, hydrodynamic force, relative velocity.

Introduction

Advantages/disadvantages of an upright posture

For many marine benthic organisms an upright posture in the water column is important for performance. An upright posture exposes organisms to faster water velocities higher in (or above) the benthic boundary layer, enhancing rates of mass transfer of essential gases and nutrients (e.g. Wheeler, 1988; Patterson et al., 1991; Atkinson and Bilger, 1992). For photosynthetic organisms, an upright posture may reduce shading by neighbors (e.g. Hay, 1986; Holbrook et al., 1991; Wing and Patterson, 1993), and can increase the amount and intensity of light intercepted, as light is absorbed and scattered with depth (Mann and Lazier, 1996). The greater the water velocity an organism experiences, the thinner the boundary layer between the surface of the organism and the ambient flow, and rates of mass transport across this boundary layer are faster (e.g. Koch, 1994; Gonen et al., 1995). At the same time, however, momentum transfer from ambient water to an organism's surface is also greater across thin boundary layers and can increase hydrodynamic forces experienced by the organism. Thus, there are trade-offs between the advantages (increased uptake rates and light interception) and the disadvantages (increased hydrodynamic forces) of maintaining an upright posture in moving water.

Mechanisms to maintain an upright posture

Aquatic organisms can maintain upright postures by two mechanisms: (1) having high flexural stiffness, or (2) by being buoyant. The flexural stiffness (*EI*) of a structure is a measure of the resistance of that structure to bending, and depends on both the cross-sectional dimensions of the structure, measured as the second moment of area (*I*), and on the stiffness (resistance to deformation) of its material, measured as the elastic modulus (*E*) (Wainwright et al., 1976). Buoyancy maintains an organism in an upright position by imparting a net upward force that functions to maintain it in and restore it to its erect position. Buoyancy in marine algae is usually produced by pneumatocysts (air bladders) in blades, although other mechanisms exist such as porous, honeycomb-like tissue that traps and retains gas within it (Stevens et al., 2002). The buoyancy of an organism, then, is a function of the volume of its pneumatocysts and the density of its tissue relative to the density of the water in which it is immersed. Although both buoyancy and flexural stiffness maintain benthic organisms in upright positions, these mechanisms (an upward restoring force *vs* resistance to deflection) may have different hydrodynamic consequences for upright benthic marine organisms.

In steady unidirectional flow, drag is experienced by organisms as they are pulled in the downstream direction by water moving around them. To escape high water velocities and forces, organisms that can bend may be pushed down toward the substratum into slowly moving water lower in the boundary layer. Organisms may also be reconfigured into streamlined shapes by water motion, reducing the projected area exposed to the flow and the width of their downstream wake and the drag experienced (e.g. Koehl, 1984; Koehl and Alberte, 1988; Vogel, 1994). Thick boundary layers can form on the surfaces of organisms in slow steady unidirectional flow and can present a barrier to gas and nutrient transfer from the ambient water to the organism (e.g. Patterson and Sebens, 1989; Koch, 1993; Hurd and Stevens, 1997).

In waves, organisms are exposed to a periodic reversal of flow velocity. Stiff upright organisms that do not move with the flow can be subject to drag, and acceleration reaction forces. Drag is proportional to the square of the velocity of water relative to the frond and acceleration reaction is proportional to its acceleration, and the magnitude of these forces changes as flow accelerates and decelerates past an organism (Denny, 1988). Flow reversal in waves can disrupt boundary layers that form over the surface of the organism, and the exchange of gases and nutrients to and from an organism may be enhanced in turbulent or thin, newly forming boundary layers (e.g. Koch, 1994; Stevens et al., 2003; Reidenbach et al., 2006). Thus, wavy habitats have the potential to be hydrodynamically challenging for organisms trying to remain attached to the substratum, but can be rewarding in terms of increased potential for mass transfer for organisms that are able to persist (Norton et al., 1981; Carpenter et al., 1991; Falter et al., 2005).

Objectives of this study

This study was conducted to address the following question. What are the effects of different magnitudes of *EI* and buoyancy on hydrodynamic forces and relative velocity on a benthic alga in unidirectional and wavy flow?

I addressed this question using *Turbinaria ornata* (Turner) J. Agardh, a brown macroalga that uses either buoyancy or flexural stiffness to maintain an upright position in very different flow habitats. *Turbinaria ornata* is abundant across reef systems throughout French Polynesia (Payri and N'Yeurt, 1997). Fronds of *T. ornata* in calm backreef habitats have flexible stipes and airbladders that make them buoyant. Fronds in forereef habitats exist under waves and are stiff, do not possess airbladders, and are not buoyant (Stewart, 2004). The production of airbladders is a plastic trait that can be induced by transplanting forereef fronds to calm backreef sites (Stewart, 2006a). Buoyancy of backreef fronds increases with reproductive maturity, corresponding also with decreases in stipe strength and extensibility (Stewart, 2006b), contributing to the potential for rafting of mature buoyant fronds that is an important dispersal mechanism for this alga (Payri and Stiger, 2001). In addition to differences in *EI* and buoyancy, forereef

and backreef fronds also differ morphologically in other ways, forereef fronds exhibiting 'dwarfism' in relation to backreef fronds (Payri, 1984). Backreef fronds are longer, have a longer bladed portion, thinner stipes and shorter blades than forereef fronds (Stewart, 2006a).

A previous study examined the hydrodynamic effect of the two naturally occurring levels of *EI* and buoyancy of *Turbinaria ornata* in the field, and found that these differences in *EI* alone did not result in different hydrodynamic consequences, but that the combination of the *EI* and buoyancy of backreef fronds resulted in lower force and relative velocity than experienced by forereef fronds in waves (Stewart, 2004). This study expands upon that work by using physical models of *T. ornata* to explore degrees of *EI* and buoyancy beyond that available in real algae. Using these models in controlled flow environments in the laboratory, I investigate the general mechanisms responsible for differences in hydrodynamic force experienced by buoyant and stiff fronds in both unidirectional and wavy flow.

Materials and methods
Model making
Original casts from live algae

Models of typical adult backreef and forereef algae (Fig. 1) were constructed by making molds of each type of frond from plaster of Paris casting material. Fronds used to make the molds were chosen to represent the typical adult morphology from each habitat.

Construction of re-useable silicone molds

The plaster molds used to make models of fronds were from Flexane two-part epoxy (Devcon® Flexane®, Avon, OH, USA). These rubber casts were then transported back to the UC Berkeley Museum of Paleontology where they were used to construct re-useable molds from silicone (Silastic™ 'E' RTV silicone rubber, Dow Corning Company, Midland, MI, USA).

Materials for each type of model

Six types of backreef and forereef models were constructed with a range of buoyancies and *EI* values (Fig. 2). Three replicates of each type of model were constructed from both the backreef and the forereef molds. Models of forereef and backreef models differed in several morphological characteristics (Table 1). The effect of length was removed from the experiment by constructing forereef and backreef to be the same total length (14 cm).

The six types of models (very flexible, flexible, flexible non-buoyant, extra-buoyant, stiff and rigid) were constructed using the silicone molds from the following materials:

(1) Very flexible models were constructed using a two-part multi-purpose elastomer (LS-40 BJB Enterprises, Tustin, CA, USA).

(2) Flexible models were constructed from urethane two-part epoxy (77:23 mix ratio of resin to curing agent by weight)
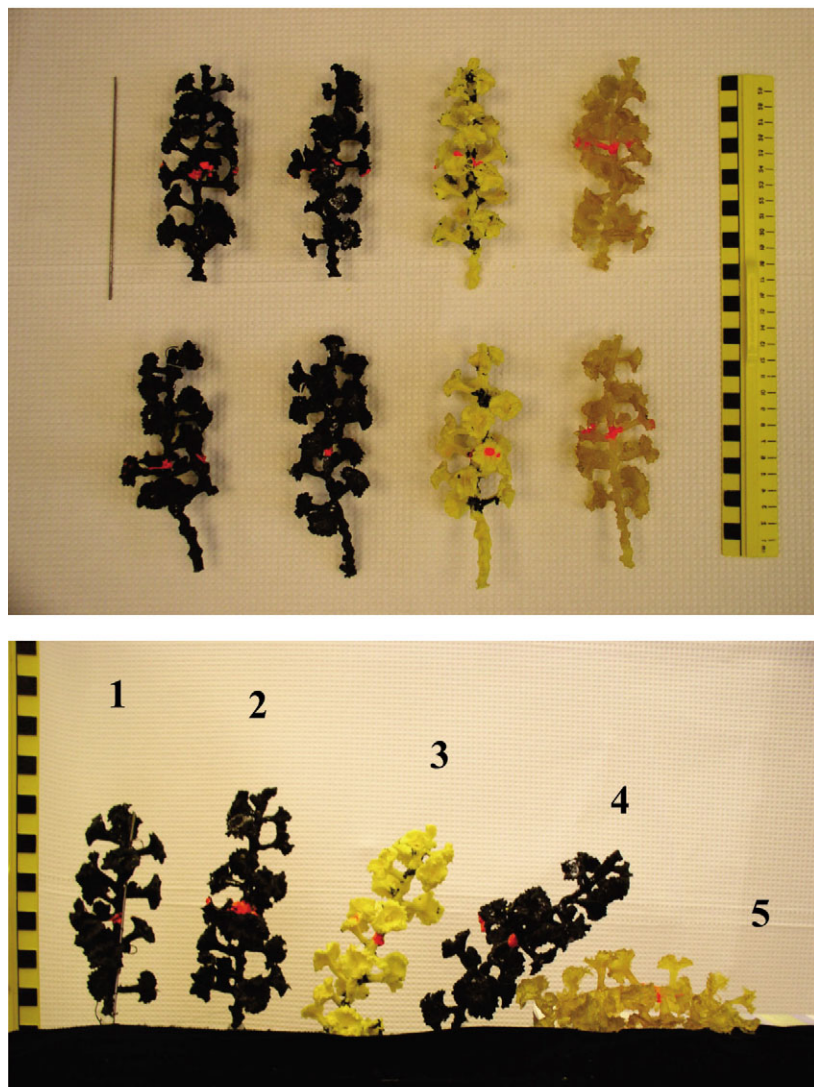
Fig. 1. Top: forereef (top row) and backreef (bottom row) models. From left to right: buoyant stiff, extra-buoyant moderately stiff, buoyant flexible and buoyant very flexible. Non-buoyant models were created by adding small lead shot to the flexible models. Rigid models were created by tying stiff models to the thin stainless steel rod at the far left of top row. Markings on ruler are in cm. Bottom: forereef models in 'upright' positions in air to demonstrate differences in stiffness. *EI* decreases from left to right: 1, rigid; 2, stiff; 3, moderately stiff; 4, flexible; 5, very flexible.

buoyant force (F_B) was determined using the equation:

$$F_B = \boldsymbol{g}V(\rho_a - \rho_w) , \qquad (1)$$

where $\boldsymbol{g}$ is the acceleration due to gravity (9.81 m s^{-2}), V is the volume of the alga, ρ_a is the density of the alga and ρ_w is the density of the freshwater that was used for all experiments in this study (998 kg m^{-3} at 20°C) (Vogel, 1994). The volume of models was determined by measuring displacement of the volume of water in a graduated cylinder. Dividing the mass of each model by its volume yielded estimates of its density. The mass of each frond was determined from the mean of two measurements (to the nearest 0.01 g) using a precision balance (Explorer model, Ohaus Corporation, Bradford, MA, USA).

Determining flexural stiffness of models

Flexural stiffness (*EI*) was determined for three stipes of each type of backreef and forereef model (Table 2). The basal portion of stipes of models (just above the holdfast) was used to determine the extension ratio (λ), as based on observations in the field this was the location on the frond where the majority of bending and breaking occurred.

Elastic moduli (*E*) were measured by conducting tensile stress-extension tests on model stipes, as described elsewhere (Koehl and Wainwright, 1977), using a materials testing machine (Model 1122, Instron Corp., Norwood, MA, USA). The extension ratio (λ) for each model was calculated using the equation:

$$\lambda = L / L_o , \qquad (2)$$

where L_o is the original length of the test portion of the stipe, and L is the length of that portion of the stipe at the time it broke. The force with which the stipe resisted the extension was measured to the nearest 0.001 N. Stress (N m^{-2}) experienced by stipes of models was calculated by dividing the force with which the stipe resisted extension by the cross-sectional area of it at the point that it broke. The diameter of each stipe at its break was measured using digital calipers to the nearest 0.01 mm and the area was calculated using the equation for the area of a circle, as stipes were roughly circular

(Devcon® Flexane®) with addition of 120 g of an additive to reduce hardness (Devcon® Flexane® Flex-add™). Flexible non-buoyant models were made by gluing 10 g of small lead shot into interstices at the end of the blades and along the stipe of flexible models. This affected their buoyancy but not their shape.

(3) Extra-buoyant models were constructed from insulating foam sealant (Dow Great Stuff® Rancho Cucamonga, CA, USA).

(4) Stiff models were constructed from Devcon® Flexane® urethane two-part epoxy (77:23 mix ratio of resin to curing agent by weight).

(5) Rigid models were created by tightly tying thin stainless steel rods to the stiff models using thread.

Note: all models were buoyant except those made non-buoyant by addition of weight.

Measuring buoyancy of models
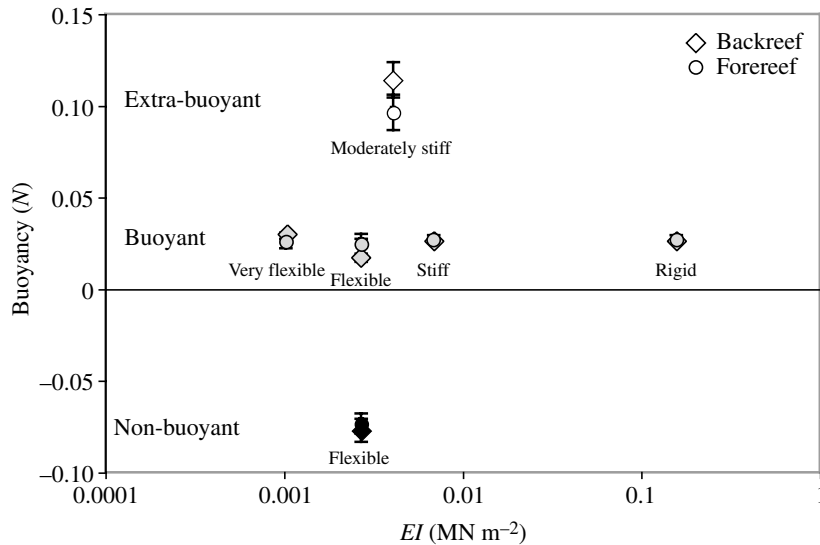
To quantify the buoyant force experienced by each model,

Fig. 2. Flexural stiffness (*EI*) and buoyancy of backreef and forereef models. Values are means ± s.d., *N*=3. *EI* of real backreef algae = 1.45×10^{-3}, and of forereef algae = 4.51×10^{-3}. Buoyancy of real backreef algae = 0.023 N, while forereef algae are negatively buoyant (–0.011 N) (Stewart 2004).

stainless steel rods to which the stiff models were attached. The *E* of the stainless steel rod was determined from published values (Wainwright et al., 1976) and the *I* of the rod was determined as above.

Water flow
Unidirectional flow

Force experienced by models in unidirectional flow was measured in a recirculating flow tank with a working section of 0.35 m×0.50 m×2.00 m described elsewhere (Martinez, 2001). Flow velocity was measured using an Acoustic Doppler Velocimeter (ADV) (Sontek, Inc., San Diego, CA, USA). The mean flow speed at each of six heights above the floor of the flume over 30 s at five motor settings (16, 32, 50, 67, 73 cm s^{-1}) were measured. Water depth in the flume was 35 cm. The velocity of the flow as a function of the height above the bottom of the flume is shown in Fig. 3.

Wavy flow

Experiments in wavy flow were conducted in a long wave tank (+15 m) with a width of 45 cm. Water depth in the tank for the experiments was 32 cm. A motorized paddle created

in cross-section. The elastic modulus (*E*) for each model was determined from the slope of the straight portion of the curve made by plotting stress *vs* extension ratio for each stipe (Wainwright et al., 1976).

The second moment of area (*I*) is a measure of the distribution of material around the axis of bending and is proportional to its radius raised to the fourth power. The *I* of each stipe was calculated using the equation for I for a circular cross-section:

$$I = \pi(d/2)^4 / 4, \qquad (3)$$

where *d* is the diameter of the stipe measured as described above.

The *EI* of the rigid model was taken to be the *EI* of the thin

Table 1. *Morphological features that differ between backreef and forereef models*

Morphometric	Backreef	Forereef	*P* value
Blade length (cm)	1.7±0.28	2.3±0.27	<0.05
Blade thickness at stipe (cm)	0.2±0.02	0.3±0.01	<0.05
Distance between blades (cm)	1.1±0.017	1.1±0.09	NS
Diameter of cross-section of model at widest part (cm)	3.9±0.36	5.1±0.31	<0.05

Values are means ± s.d., *N*=3.
All comparisons are by Mann–Whitney *U*-tests.

Table 2. *Flexural stiffness and buoyancy of backreef and forereef models*

Model type	Backreef and forereef *EI* (MN m^{-2})	Backreef F_B (N)	Forereef F_B (N)
Very flexible buoyant	0.001±8.50×10^{-6}	0.029±0.0028	0.026±0.0066
Flexible buoyant	0.003±10.20×10^{-5}	0.021±0.0107	0.025±0.0092
Flexible non-buoyant	0.003±10.20×10^{-5}	–0.077±0.0107	–0.073±0.0094
Moderately stiff extra-buoyant	0.004±1.70×10^{-4}	0.117±0.0164	0.097±0.0164
Stiff buoyant	0.007±10.20×10^{-5}	0.027±0.0044	0.027±0.0035
Rigid buoyant	0.157±1.70	0.029±0.0064	0.026±0.0035

EI, flexural stiffness; F_B, buoyancy.
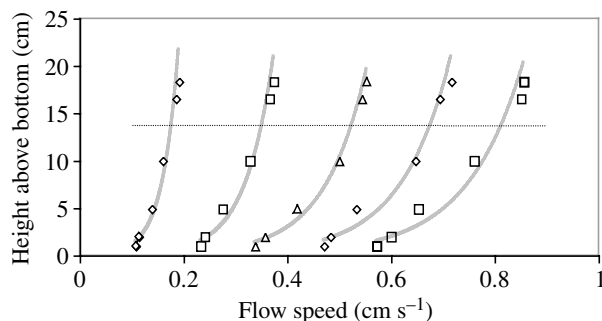Values are means ± s.d. (*N*=3 models of each type).

Fig. 3. Unidirectional water velocity to a height of 25 cm above the floor of the flume at five motor settings (indicated by different symbols and fit with logarithmic best-fit lines highlighting the velocity profile in the flume at each flow speed). The height of the upright models (14 cm) is marked by a dotted line.

waves with a 2-s period and root-mean-square and maximum velocities of 15 cm s^{-1} and 27 cm s^{-1}, respectively (Fig. 4). At the height of the upright models, water moved 30 cm in each direction per wave. Water velocity in the waves was measured at the height of the models (14 cm) using the ADV during the course of all experiments in the wave tank. Due to the refraction of the water off the back wall of the wave tank the wave had a slight asymmetry.

For logistical reasons, the waves used in this experiment were much smaller in period (2 s period) and amplitude (10 cm) than the waves that *T. ornata* experiences in the field (8–10 s period with amplitudes ~0.5–1 m and larger during storms). While the horizontal displacement of water in waves in the tank is shorter than under waves on the reef, its is 30 cm in each direction, just longer than twice the length of the models (2×14 cm) indicating that water in the wave tank did move further in each direction than the potential maximum displacement of the models but to a lesser degree than water moves on the forereef. The results of this experiment are not intended to be directly applicable to a forereef of a barrier reef, but to provide a common wave field to identify general mechanisms by which morphology, stiffness and buoyancy affect hydrodynamic performance. Therefore the implications
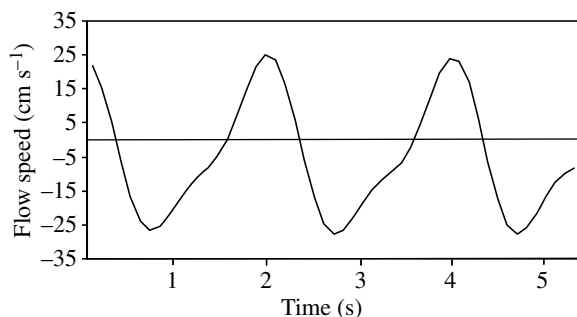
of results from the wave tank are discussed in a general context of oscillatory flow.

Force measurements

Force experienced by the models was recorded using a force transducer made according to a published design (Koehl, 1977) and details of its construction are reported elsewhere (Stewart, 2004). The force plate was situated under a false bottom in the flume so that only a 1 cm high sting extended up into the flow. Models were attached at the base of their stipes with a single cable tie as low as possible to the sting of the force transducer so as to not affect the bending of the model. The response time of the force transducer was 0.01 s. Voltages from the force transducer were recorded at 10 Hz using Biobench^{TM} software (National Instruments, Austin, TX, USA) on a laptop computer *via* a bridge amplifier and a DAQ 1200 card (National Instruments).

Force transducers were calibrated by hanging weights from a string attached to the transducer, which sat horizontally on a table. The string was laid over a pulley attached to the edge of the table so that the mass of the weight caused a horizontal displacement of the transducer. Weights ranging from 0.01 N to 2.0 N were hung from the transducer in both the positive and negative directions. Each weight was hung three times and the mean of the voltages registered for each weight was used to calculate a linear regression (r^2=0.88) for the voltages measured as a function of force.

Measurements of motion of models

A video of the motion of the models in the oscillatory flow was recorded on a digital video recorder at 60 frames s^{-1} during the force experiments at 60 frames s^{-1}. Video was synchronized with the force recordings using an event marker, which consisted of a small LED light that was illuminated in front of the video camera for several seconds at the beginning of each run, simultaneously putting a visual marker on the video and a voltage spike on the recordings of the water flow and force. This enabled synchronization of video frames with voltage signals from the force transducer.

The movement of the distal tip of each frond was digitized at 0.1-s intervals from the video using Motus^{TM} Peak 3.0 software (Inition Ltd., London, UK) for 20 s of each trial. Because the motion of the very flexible models differed a great deal along the length of the model, a second point mid-way along the length of the model (7 cm from the tip) was also digitized. This positional data was then converted to instantaneous velocity by taking the difference in position between intervals and dividing by 0.1 s. Calculations were done using Matlab 6.5 software (The Mathworks Inc., Natick, MA, USA).

Relative velocity calculations

The relative water velocity past the surface of each model was estimated using the simultaneous video recording of the model and the flow velocity recordings during each trial. For each 20 s trial, algal velocity was subtracted from the corresponding water velocity for the same instant, giving an

Fig. 4. Velocity profile of flow in wave tank at 14 cm (the height of the models) over time.
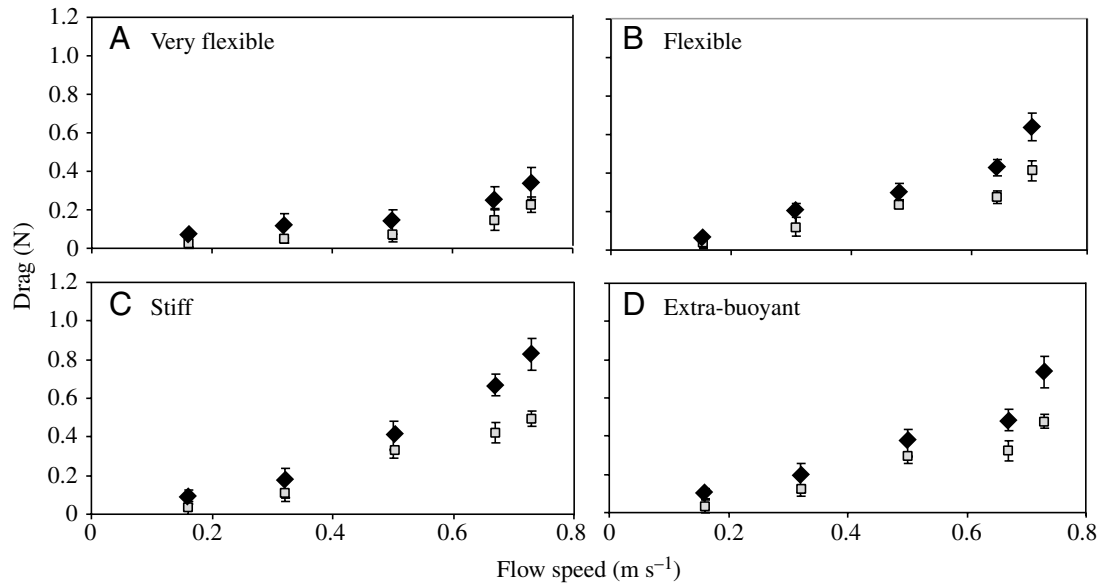
Fig. 5. Drag force experienced by forereef (filled symbols) and backreef (open symbols) shapes of (A) very flexible models, (B) flexible models, (C) stiff models and (D) extra-buoyant models at increasing unidirectional flow speed. Data are not shown for non-buoyant or rigid models as these comparisons were made by adding lead shot to stiff models, and attaching a steel rod to stiff models, altering their buoyancy and flexural stiffness but not their shape.

estimate of the water velocity relative to the frond during each 0.1 s interval. Because the flow velocity was measured at a constant height of 14 cm, and models moved in the flow and were not always upright, relative velocities may overestimate velocity, particularly for flexible models when they were bent over into slower moving flow in the boundary layer in unidirectional flow. However, because the conclusions drawn from these experiments are expressed as relative patterns they will not be affected by this slight overestimation. Because

both the water and the alga exhibited oscillatory movement in the waves, velocities were recorded as positive (toward the left as viewed through the digital camera) and negative (toward the right) values. Data of water velocity, force, the position of the model and relative velocity at the surface of the model for each model were then synchronized for comparison.

Index of compaction

Streamlining of blades and compaction of overall fronds in moving water can reduce the area of an organism projected into the flow and its downstream wake, thereby reducing the drag it experiences. To estimate the degree of compaction of each model, the width of bladed portion at the mid-point of the model at the lowest flow speed (16 cm s^{-1}) (at which speed the blades had not reconfigured) was compared with the width at the same point on the frond at the highest flow speed (73 cm s^{-1}). Width measurements were made using NIH Image (Scion Corporation, Frederick, MD, USA) from frames of video of each trial with a precision of 0.01 cm. Values for models of each type were averaged (*N*=3). High values of the
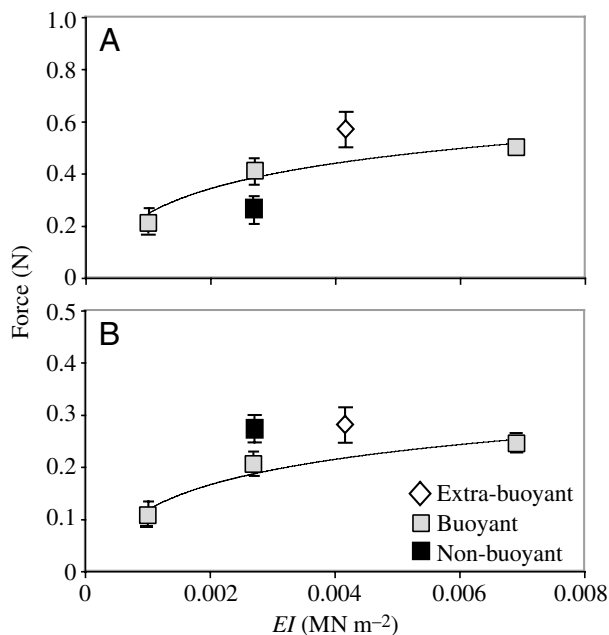

Fig. 6. (A) Drag force experienced by models as a function of *EI* at the highest unidirectional flow speed (0.73 m s^{-1}) for all models (excluding rigid models). Values are means ± s.d., *N*=6. Values for extra-buoyant and non-buoyant models fall above and below the best-fit logarithmic trend lines fit to data from buoyant models, respectively. (B) The maximum force experienced by models in waves for all models excluding rigid models (means ± s.d., *N*=6). Values for extra-buoyant and non-buoyant models fall above the best-fit logarithmic trend lines fit to data from buoyant models.
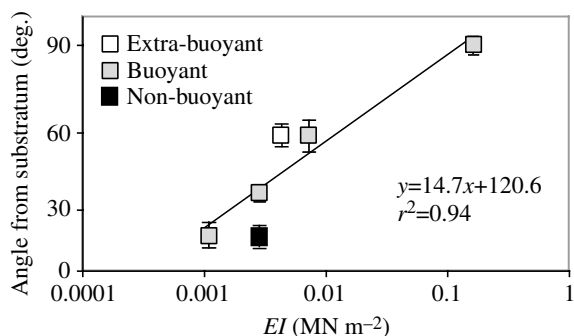
Fig. 7. Angle of deflection of models of increasing *EI* at the highest unidirectional flow speed. Values are means ± s.d., *N*=3. Upright posture is 90°. Non-buoyant models deflect more than buoyant models of the same *EI* as determined by Kruskall–Wallis non-parametric analysis (*H*=33.56, d.f.=11, *P*<0.05). Extra buoyant models deflect less than predicted by best-fit trend lines fit to data from models that vary in *EI*.

ratio of the compacted width to the width at the lowest flow speed indicate that the model did not compact very much, whereas low values indicate that it did.

Statistical analysis

All statistical analyses were conducted with SAS Statview (v.5 SAS Institute, Cary, NC, USA), and significance determined by *P* values <0.05.

Results
Unidirectional
Effect of flow speed

Drag force experienced by models increased with flow speed (Fig. 5). Differences between models were most evident at the highest flow speed (0.73 m s^{-1}) and the following results of the
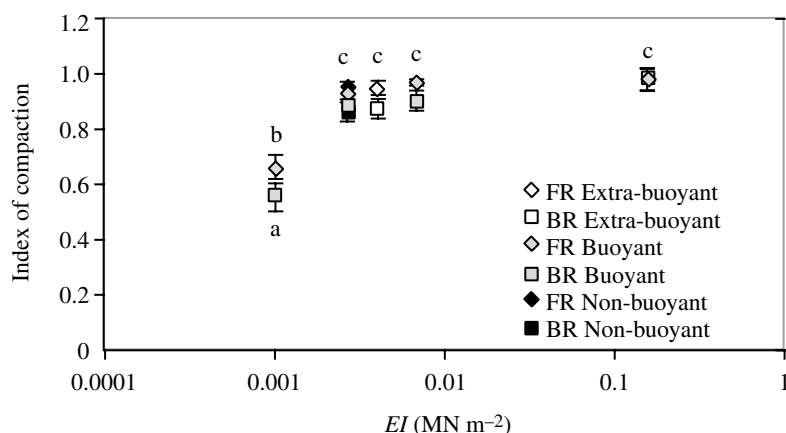

Fig. 8. The index of compaction of all models at the highest unidirectional flow speed (73 cm s^{-1}). Values are means ± s.d., *N*=6. Only the most flexible models were significantly compacted, and backreef models more so than forereef models, as determined by Kruskall–Wallis non-parametric analysis (*H*=30.23, d.f.=11, *P*<0.05) and Nemenyi *post-hoc* multiple comparisons (Zar, 1999). Letters that are different indicate significant differences between groups as determined by Nemenyi *post-hoc* multiple comparisons (Zar, 1999).
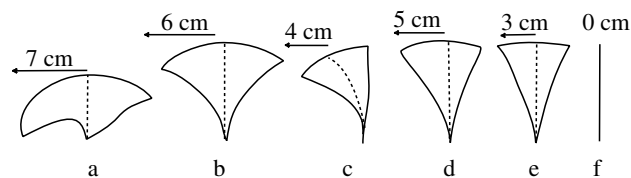

Fig. 9. Tracings of the motion of models of each type in waves. Arrows indicate the distance the tip of the model moved from its upright position (dotted line) in one direction per wave (not to scale). a, very flexible, buoyant; b, flexible, buoyant; c, flexible, non-buoyant; d, stiff, extra-buoyant; e, stiff, buoyant; f, rigid buoyant.

experiments conducted in unidirectional flow focus on data obtained at this speed.

Effect of morphology

Drag force experienced by forereef models was higher than that experienced by backreef models at the higher flow speeds in the unidirectional flume for all models except the very flexible ones (Fig. 5).

Effect of EI

Drag force increased with *EI* for backreef and forereef fronds (Fig. 6A). The amount the models deflected downstream in the flow increased with decreasing *EI* (Fig. 7). At the highest flow speed, the width of the bladed portion of the most flexible models was ~60% of their width at the lowest flow speed, indicating that they were compacted by the water moving around them. Other models were not compacted significantly, even at the highest flow speed (Fig. 8).

Effect of buoyancy

Buoyant models experienced higher forces (Fig. 6A) and deflected less in unidirectional flow (Fig. 7) than their non-buoyant counterparts of the same *EI*.

Waves
Effect of morphology

There were no differences in any results of the experiments in waves attributable to different morphology of backreef and forereef models (data not shown). Therefore, the following results combine data obtained from backreef and forereef models.

Effect of EI

Models of higher *EI* experienced higher force in waves than models of lower *EI* (Kruskall–Wallis *H*=29.09, d.f.=5, *P*<0.05) (Fig. 6B). How much a model moved with the flow affected the force it experienced. Models that moved during the fastest flows and stopped moving after the peak velocity of the wave cycle had passed experienced lower relative velocities and lower forces than those that

Fig. 10. (A) Water velocity and model position during the passage of a wave. For water velocity, positive numbers indicate the water is moving in one direction in the wave tank, and negative numbers indicate that the water is moving in the other direction. In each direction the water speed increases to a maximum velocity and then slows down before reversing and going in the other direction. Position indicates the distance deflected by the model at a particular water velocity. (B) Position of stiff and flexible models during the passage of a wave. Stiff models are deflected the maximum distance during high velocities, and begin to right themselves as the flow slows. Flexible models are deflected the maximum distance just before the flow begins to move in the opposite direction. (C) Position of models of various levels of buoyancy during the passage of a wave. Extra-buoyant and non-buoyant models are deflected less during each wave than are moderately buoyant models, and are extended in the direction of flow during higher velocities than are moderately buoyant models.
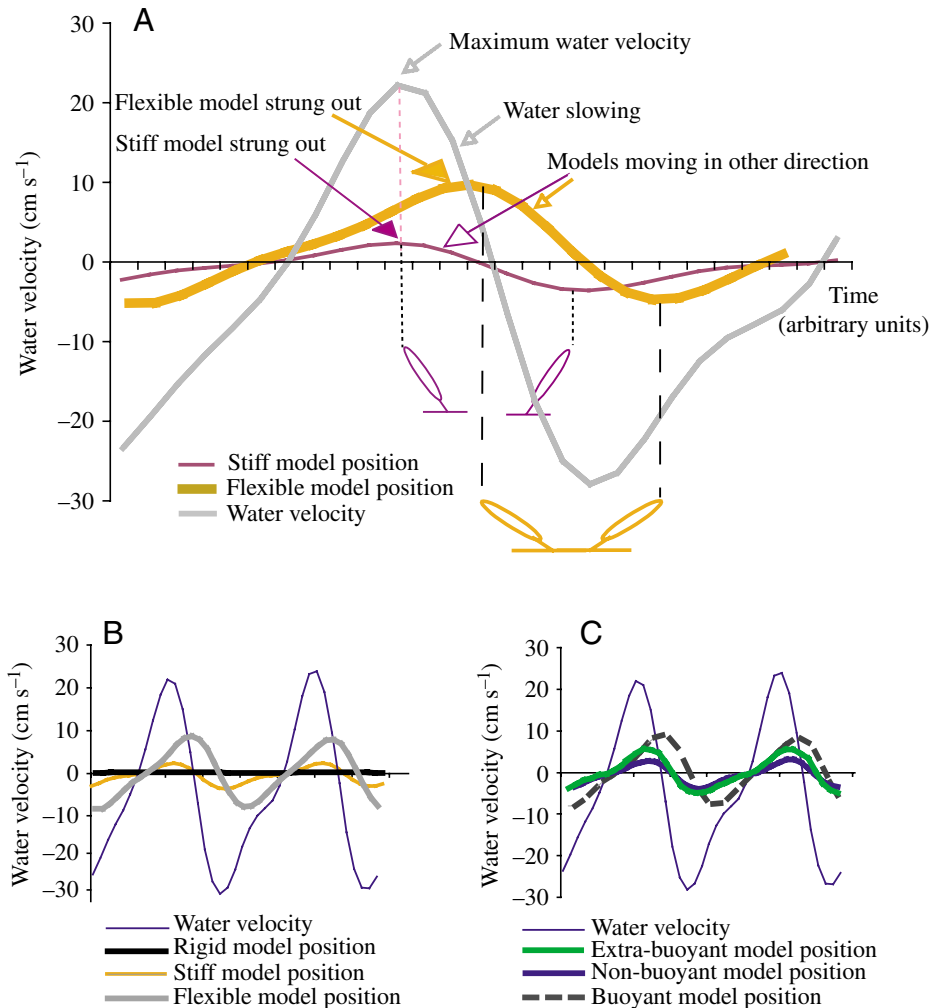
stopped moving with the flow at faster flow velocities. Stiffer models moved shorter distances in each wave than did more flexible models (Fig. 9). The timing of the movement of the model, with respect to water velocity, also differed with flexural stiffness (Fig. 10). Stiffer models only moved with the fastest flows, and when flow slowed down, stiff models began to right themselves. Flexible models moved with fast flows and kept moving as flow speed decreased. The most flexible models

moved with even the slowest flows and kept traveling in the direction of flow for the entire time the water moved in one direction (Fig. 11).

All models except the very flexible models moved in waves as one unit, the tip moving in line with the rest of the model. However, the most flexible models had portions moving in different directions as they experienced whiplashing. Whiplashing occurs as the basal portion of a
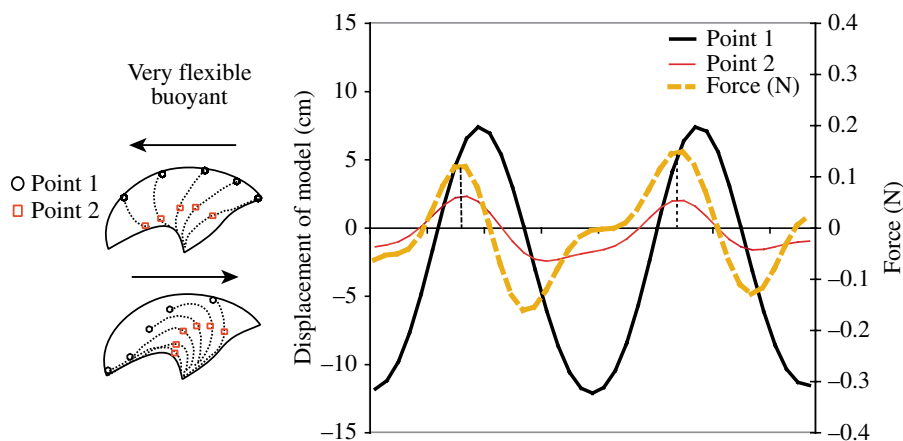

Fig. 11. Force and position of points 1 and 2 on a very flexible model during waves. Models of the lowest flexural stiffness experienced whiplashing (see text for explanation) where the tip of the model lagged behind the middle portion. Maximum force is experienced when point 2 is displaced the furthest (highlighted by dotted line). Maximum displacement of point 1 occurs after the model experiences peak force. *x* axis is time in arbitrary units.

long, flexible structure becomes fully extended in the direction of flow, decelerates to a halt but the distal portion keeps moving and accelerates as occurs when cracking a whip. This occurs because of conservation of angular momentum, which is proportional to angular velocity multiplied by the mass of an object. Along the length of an object there is progressively less mass towards its tip, and as mass decreases, angular velocity increases. Consequently, the tip of an object can move faster than the surrounding fluid even after the basal portion has stopped moving, or has even begun to move in the opposite direction. In the very flexible models, the tip (point 1) of the model lagged behind the middle of the model (point 2) (Fig. 11). The tips of the models were whipped forward and back and at times were moving faster than the ambient water. These very flexible models experienced maximum forces at their bases when the middle of the model (point 2) was pulled in the direction of flow. Tips of very flexible models were extended in the direction of flow after the maximum force was experienced (Fig. 11).

The relative velocity at the surface of the distal tip of the model at the time of peak force increased with increasing EI of models (Fig. 12). Relative velocity of the very flexible models was negative because the tips (point 1) of the models were moving faster than the surrounding water at the time of peak force.

Effect of buoyancy

The buoyancy of models affected the force they experienced. Both extra-buoyant and non-buoyant models experienced similar drag to stiff models in waves. Forces experienced by extra- and non-buoyant models were higher than those experienced by moderately buoyant models (Fig. 6B). Extra-buoyant and non-buoyant models moved less from the positions they adopted in still water than buoyant models did (Fig. 9). Extra-buoyant models were moved only in high velocities and began to right themselves as the water velocity slowed, whereas moderately buoyant models continued to move as the flow slowed (Fig. 10).
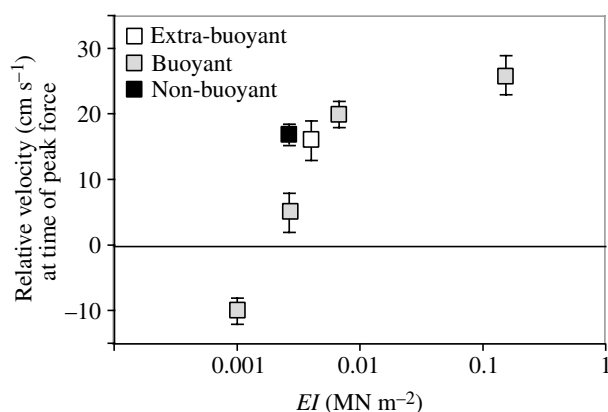
Non-buoyant and extra-buoyant models experienced higher relative velocities at the time of peak force than buoyant models of the same EI (Fig. 12).

Discussion
Flexural stiffness
Stiffness in unidirectional flow and waves

As observed in this experiment, organisms with high flexural stiffness (EI) generally experience higher relative water velocities and forces in unidirectional flow and in waves than do more flexible organisms (e.g. Alben et al., 2002; Bouma et al., 2005). In unidirectional flow, stiffness reduced the amount that models deflected, exposing them to faster water higher in the boundary layer, and reduced the amount that models were reconfigured into streamlined shapes by moving water. As drag force is proportional to the plan area of an organism (Denny et al., 1985), the upright, un-streamlined shapes of stiff models resulted in higher drag than deflected, compacted flexible models. In waves, stiffness reduced the amount that models moved with the water, increasing the relative velocities at their surfaces and the drag that they experienced.

To persist in high-flow habitats, stiff organisms must have other attributes to prevent being dislodged. Stiff organisms in areas of rapid unidirectional flow or high-energy waves might be expected to be small, and in general, many organisms in high-flow habitats are shorter than their counterparts in calm habitats (e.g. Norton et al., 1981; Blanchette, 1997; Stewart and Carpenter, 2003). *Turbinaria ornata* in high-energy forereef habitats is stronger (Stewart, 2004), and has a morphology that is shorter with thicker stipes and blade attachments, and fewer blades than fronds from calm backreef habitats (Stewart, 2006a). Aggregation may also provide a strategy for survival in high flow, as high drag experienced by individuals can translate into modification of the physical environment *via* reduction of hydrodynamic energy in aggregations (Jackson and Winant, 1983; Worcester, 1995; Jackson, 1997; Johnson, 2001). For example, stiff seagrass dissipates up to three times as much wave energy as flexible seagrass at densities of 450–1850 individuals m^{-2} (Bouma et al., 2005).

Flexibility in unidirectional flow

In unidirectional flow, organisms with low EI encounter velocities approaching ambient velocity because they are strung out in the direction of flow and are not moving with it (Koehl, 1984). However, flexibility allows organisms to be reconfigured into streamlined shapes in moving water, potentially reducing the drag force that they experience (e.g. Koehl and Alberte, 1988; Carrington, 1990; Gaylord et al., 1994). Flexible organisms may also lie along or be pushed down to the substratum, where they may experience reduced flow velocities low in the boundary layer and avoid high relative velocities and forces (Koehl, 1984). This may also decrease the moment arm of the imposed force, effectively reducing the stress experienced by deflected organisms (Gaylord and Denny, 1997). However, organisms low in the boundary layer may face

Fig. 12. Relative velocity of models at time of peak force in waves as a function of EI. Values are means ± s.d., N=6.

transport limitation in slow water velocities (Boynton et al., 1981; Wheeler, 1988; Stewart and Carpenter, 2003). Flexible seaweeds may ameliorate mass transfer limitation by the fluttering of their blades, which disrupts boundary layers on their surfaces but may also increase the force that they experience (Koehl and Alberte, 1988).

Flexibility in waves

Flexible organisms can move back and forth in the bi-directional flow under waves. During the time an organism moves with the flow, it experiences low relative velocities at its surface as it moves along at ambient velocity, and rates of mass transfer may be reduced as nutrients and gases are depleted from surrounding water. However, if an organism moving with the flow becomes extended in the direction of flow before the flow reverses, the relative velocity will increase as water continues to pass by. Due to the short period of waves in the tank, the flexible and very flexible models moved with the flow for most of their excursion in each direction, as would longer seaweeds in large waves.

This 'going with the flow' strategy reduced the force experienced by these models in waves. As a flexible organism moves with the flow, little force is imposed during this portion of the cycle (Koehl, 1986). However, by moving with the flow an organism gains momentum, and this can impose an inertial force if the organism reaches the end of its tether before the flow reverses and is jerked abruptly to a halt (Denny et al., 1998). Such inertial forces can be high if the organism is moving rapidly when it is jerked to a halt and when a large proportion of the mass of the organism is situated at its end (Friedland and Denny, 1995). Inertial forces were not experienced by any of the models in this experiment due to the relatively slow velocity of the waves in the wave tank, and the even distribution of mass along the length of models. However, dependent on the type and velocity of flow, the wave period and amplitude, the length, flexibility and distribution of mass along the stipe, inertial jerk forces can be substantial, and the effect of 'going with the flow' may alternatively decrease or increase the forces experienced by flexible organisms in waves.

In this experiment whiplashing reduced the force experienced at the bases of the most flexible models. Ends of whiplashing models moved in the opposite direction to the flow because the water had reversed by the time the tips of the models were completely pulled to their full length in one direction. This resulted in the tips of these models moving faster than the surrounding water and negative relative velocities at the tips of these models resulting in low force experienced in waves. However, at higher oscillatory velocities, whiplashing may lead to tattering or tearing as the ends of the frond are snapped, similar to the way a whip cracks (Gaylord and Denny, 1997).

Effect of buoyancy
Cost of buoyancy

Buoyancy is a mechanism that produces upright postures in marine organisms without investing much energy into structural support. However, production and maintenance of buoyancy may have associated costs. For example, reduced photosynthetic rates have also been noted in algal blades possessing pneumatocysts relative to those without (Kilar et al., 1989). Therefore, if both stiffness and buoyancy impose costs to an organism while both function to maintain its upright position in the water column, it is not surprising that stiff, buoyant organisms are uncommon in nature. Buoyant organisms tend to be flexible. The consequences of buoyancy to hydrodynamic forces depend on the degree of buoyancy and the type of flow an organism experiences.

Moderate buoyancy

A moderate level of buoyancy (defined here as just enough to impart positive buoyancy) does not prevent a flexible organism from moving with the motion of the water around it, but functions to return an organism to an upright posture as the flow slows. Moderate buoyancy is an effective strategy in areas of low or moderate unidirectional flow, where maintaining an upright posture allows organisms to take advantage of faster flow higher in the boundary layer, enhancing mass transfer. Examples of such areas include areas exposed to tidal currents where water flows for hours in one direction before reversing, and in backreefs where water passes over the reef crest and moves in one direction to the mouth of an adjacent bay, creating unidirectional flow through the backreef.

Buoyancy, combined with flexibility, can create a buffer against high forces for organisms that are exposed to periodic pulses of high water velocity (e.g. occasional waves in areas dominated by tidal currents), or in waves. During periods of high flow they can be pushed down into the slower flow close to the substratum, where they may escape high hydrodynamic forces, but are righted by their buoyancy after the flow slows. By this mechanism, flexible, moderately buoyant organisms can resist dislodgement during occasional or periodic high-flow events without investing additional resources in structural support.

By providing a mechanism to return an alga to an upright posture after it has compacted in response to water motion, buoyancy may also increase light interception. Compaction of fronds or thalli into streamlined shapes can lead to self-shading of blades layered on top of one another. Passive righting and spreading of compacted blades can help to maximize light interception for plants that may be exposed to frequent pulses of high velocities (Harder et al., 2004).

The combination of moderate buoyancy and flexibility may also be an effective mechanism in areas where the height of the water changes due to tidal exchange, as this combination enables organisms to remain at or near the surface of the water throughout the tidal cycle without the danger of becoming exposed to the air at low tide, as might happen with a stiff organism taller than the water depth at low tide.

High buoyancy

Extra-buoyant models used in this experiment had buoyant forces 5× higher than real fronds and the results show that they behaved like stiff models in the amount they were deflected,

and in the timing of their movement relative to peak forces in both unidirectional flow and in waves. Because very high buoyancy can result in high forces in moving water, this is not a strategy well suited to high-flow habitats. As with *T. ornata*, other buoyant seaweeds in high-flow areas have also been reported to have reduced buoyancy *via* air bladders that are absent or smaller than those of their counterparts in calm habitats (Burrows and Lodge, 1954; Chapman, 1961; Jordon and Vadas, 1972; Russell, 1978). In some species, airbladders may also have more streamlined shapes in high-flow environments (Bergquist, 1959).

In addition to affecting hydrodynamic forces, buoyancy also imparts tensile forces on organisms that add to the total force contributing to potential detachment from the substratum. In *T. ornata* the buoyant force is small relative to the hydrodynamic force experienced by the frond in moderate flow (Stewart, 2004). However, as buoyancy increases so too does tensile force, and in extra-buoyant organisms the tensile force could become substantial. The upward component to total force contributed by buoyancy may act to reduce whiplashing of flexible organisms (Stevens et al., 2002), as high buoyant forces function to stretch a flexible organism toward the surface, extending it and making it move more as a single unit, reducing whiplashing.

Not buoyant

Flexible organisms that are not buoyant face the possibility of not being able to support their own weight or right themselves after being pushed over by water motion. This can be advantageous for reducing hydrodynamic forces in rapid unidirectional flow where organisms can escape high velocities low in the boundary layer. However, they face the potential problems of shading and mass transfer limitation.

The present experiment highlights the fact that the effect of non-buoyancy on hydrodynamic force depends on the relative degree of non-buoyancy, the flexural stiffness of the organism, and the type of water flow that the organism experiences. In waves, non-buoyant flexible organisms that cannot support their own weight and flop to the substratum may accrue some advantage by being able to sweep the substratum around them, dislodging young plants and other potential competitors for space (Black, 1974; Velimirov and Griffiths, 1979). Depending on the stiffness of non-buoyant organisms and the flow velocity they experience, they may slump down onto the substratum or they may just slump a bit to one side, as was the case for the non-buoyant models in this experiment, because the flow velocities in the wave tank were not sufficient to push the non-buoyant models over. If the velocity of the water in the wavy flow had been higher or the non-buoyant models used in this experiment had been more flexible, then the non-buoyant models might have been pushed over further toward the bottom. However, the non-buoyant models in this experiment were stiff enough to stay upright in the waves used in this experiment. They therefore experienced high relative velocities and forces, similar to stiff models in waves.

Conclusions

Upright postures are important for light interception and mass transfer of benthic organisms. However, an upright posture can also expose organisms to hydrodynamic forces that may be detrimental. Both *EI* and buoyancy are mechanisms to maintain upright postures in water, and each has different hydrodynamic consequences in unidirectional flow and waves. Stiff algae experience high forces in moving water, but if they are also strong they can persist in areas where mass transfer of nutrients and gases is enhanced by fast flow. Buoyancy can have similar consequences to stiffness for relative water velocities and hydrodynamic force, because both mechanisms reduce the amount the organism is deflected in the direction of moving water. However, as flow speeds increase and hydrodynamic forces overcome the ability of a buoyant or stiff organism to maintain its upright posture, a stiff organism may break, whereas buoyancy enables an organism to 'rebound' back to an upright posture after it has been pushed over by moving water.

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