RESEARCH ARTICLE

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Morphological variation and phenotypic plasticity of buoyancy in the macroalga *Turbinaria ornata* across a barrier reef

Abstract Many aspects of morphology of benthic algae (length, surface area-to-volume ratio, and blade undulation) are plastic traits that vary in response to physical factors (such as light or water flow environment). This study examines whether frond buoyancy is a plastic trait, and whether differences in morphology including buoyancy affect the potential persistence of macroalgae in habitats characterized by different water flow regimes. Fronds of the tropical alga *Turbinaria ornata* in protected backreef environments in Moorea, French Polynesia possess pneumatocysts (gas-filled floats) and experience positive buoyant forces, whereas fronds in wave-exposed forereef sites either lack pneumatocysts entirely or have very small, rudimentary pneumatocysts and experience negative buoyant forces. Forereef fronds transplanted to the backreef developed pneumatocysts and experienced increased buoyant force indicating that buoyancy is a phenotypically plastic trait in *T. ornata*. In comparing the potential for dislodgement by drag, drag was greater on forereef fronds at low flow speeds as these fronds were stiffer and did not bend over at low flow speeds and therefore were less streamlined in the flow than backreef algae, which bent easily. The environmental stress factor (ESF) (a measure of the likelihood of detachment for a frond in its habitat) was higher for forereef than backreef fronds at all flow speeds. When examined with respect to the flow velocities likely in their respective habitats however, the chance of detachment for backreef and forereef was similar. Neither backreef nor forereef fronds were predicted to break under normal, non-storm conditions, but both were

predicted to break in storms. Strong forereef morphologies are well suited to habitats characterized by rapid flow, whereas the weaker, buoyant, tall backreef fronds are well suited to habitats where crowding and shading is common but hydrodynamic forces are low.

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Introduction

Effects of frond morphology on hydrodynamic forces and danger of breaking

Water motion exerts hydrodynamic forces on benthic algae. The force experienced by an alga is a function of the interaction between its morphology and the flow it experiences in its habitat. This interaction can be affected by the alga's size, shape, and the way in which it deforms in moving water (Carrington 1990; Koehl 2000). Large algae generally experience higher forces than small algae (Dudgeon and Johnson 1992), but many algae are reconfigured into streamlined shapes by water moving around them, reducing the drag force they experience (Koehl 1984, 1986; Carrington 1990). The extent to which an alga can be reconfigured depends on its shape and material properties: thin, flexible fronds can be streamlined more easily than stiff, bushy fronds. Flexible algae may also be pushed toward the substratum by moving water, and into slowly moving water lower in the benthic boundary layer, thereby reducing the velocity and the consequent hydrodynamic forces they experience.

Changes to morphology through development and ontogeny, and through phenotypically plastic responses to physical factors can change the forces algae experience in their habitats. The environmental stress factor (ESF, sensu Johnson and Koehl 1994) is a measure of the resistance to detachment of an organism at a particular time in its ontogeny, in its habitat. For algae, it is the ratio of the strength of its stipe or holdfast (whichever is weaker) to the stress (force/cross-sectional area where force is experienced) from hydrodynamic forces.

If the ESF is greater than 1, the alga will remain attached to the substratum. If the ESF is less than 1, then the frond will detach. Through morphological variation (Johnson and Koehl 1994) and changes to tissue strength through ontogeny (Stewart 2006), the likelihood of detachment from the substratum can be similar for very different morphotypes of algae, in very different habitats at different stages of their lifecycles across seasons.

Within species differences in morphology in different flow habitats

Many seaweeds exhibit morphological variation in response to water motion (reviewed in Koehl 1986; Hurd 2000; Stewart and Carpenter 2003). Morphological attributes in calm water include undulations (Gerard and Mann 1979; Koehl and Alberte 1988), high surface area/volume ratio (SA/V) (e.g. Littler and Littler 1980; Stewart and Carpenter 2003), and increased length relative to fronds in wave-exposed habitats (Blanchette 1997). These modifications all potentially result in increased light interception, and mass transfer of nutrients and gases to and from the algal frond (Koehl and Alberte 1988), although this has not been established in all cases (Koehl and Alberte 1988; Hurd et al. 1996; Denny and Roberson 2002). Characteristics of algae in wave-exposed sites include flat strap-like blades (e.g. Gerard and Mann 1979) that streamline easily (Koehl and Alberte 1988), and fronds with low SA/V (Stewart and Carpenter 2003), both of which can decrease the hydrodynamic force experienced by the alga and the chance that it will be dislodged from the substratum.

To gain insight into the advantages conferred by aspects of morphology to the frond in its habitat, it is important to quantify the consequences of morphological variation to performance across sites. The hydrodynamic consequences of many of the traits mentioned above have been well studied. Buoyancy is another common trait among benthic algae. Blades of buoyant algae may be kept up at the surface and spread out increasing light interception and photosynthetic rates (Koehl and Alberte 1988). Buoyancy can also reduce the forces experienced by an alga in waves (Stevens et al. 2001; Stewart 2004). However, the effect of buoyancy on survival of benthic algae is less well known.

Objectives of this study

This study was conducted to investigate the effect of buoyancy, in combination with other morphological traits, on the ESF of a tropical benthic alga, *Turbinaria ornata*, in different flow habitats. *T. ornata* is a member of the Division Phaeophyta, in the Order Fucales. The genus *Turbinaria* is pan-tropical, and species *T. ornata* is common throughout French Polynesia (Payri and N'Yeurt 1997). It thrives in both calm backreef habitats, where flow is unidirectional and relatively slow, and under waves in forereef habitats, where flow is bidirectional and much faster. Dwarfism of fronds on the reef crest has been reported (Stiger and Payri 1999), and fronds in backreef habitats have gas-filled floats ("pneumatocysts") and are buoyant, whereas fronds in wave-exposed forereef sites either lack pneumatocysts entirely or have very small, rudimentary pneumatocysts and are not buoyant (Stewart 2004).

Specifically this study addresses the questions: (1) Is buoyancy in *T. ornata* a plastic trait? (2) How do the morphologies of *T. ornata* from the backreef and from the forereef (including differences in buoyancy and other morphological traits that differ between habitats) affect performance (as measured by ESF)?

Materials and methods

Study sites

This research was conducted in forereef and backreef habitats near the Richard B. Gump Research Station, University of California at Berkeley, on the island of Moorea, French Polynesia. Adult fronds (those with reproductive structures, but not yet a high load of encrusting epiphytes, as in Stewart (2006) of *T. ornata* were collected from points selected using a random number table along transects in the forereef and backreef of the barrier reef between Cook's Bay and Oponohu Bay on the north shore of Moorea. Length of fronds collected ranged from 17-21 cm for backreef fronds and 11–16 cm for forereef fronds. Fronds were held in running seawater in shaded tanks and used within 2 days of collection.

Flow in forereef and backreef

Estimates of the maximum water velocity under waves were made using wave force meters designed to record maximum velocities as described by (Bell and Denny 1994). Three wave meters were attached to eyebolts that were attached with epoxy onto the forereef and collected after 24 h for each of 3 days and the maximum flow velocity measured by each meter was recorded. At the backreef site, the time required for neutrally buoyant particles to travel 45 cm was measured to the nearest 0.1 s to estimate flow speed. Estimates of flow in the backreef were made at midday when the waves on the forereef appeared to be biggest, so that they would correspond to forereef maximum velocity measurements. Five measurements per day were made for 3 days.

Morphometrics

Digital calipers were used to measure nine morphometric parameters (Fig. 1) to the nearest 0.01 mm for each

Fig. 1 Measured morphometric parameters of forereef and backreef fronds. **a** frond length, **b** length of the bladed portion of the frond, **c** length of unbladed stipe, **d** the diameter of the stipe just above the holdfast. **e** blade length (average of ten randomly selected on each frond), **f** the diameter of the blade at the attachment to the stipe (average of ten randomly selected on each frond), Also measured, but not diagrammed were the distance between blade attachments (average of ten randomly selected on each frond), the total number of blades, and the proportion of the total blades that contained pneumatocysts
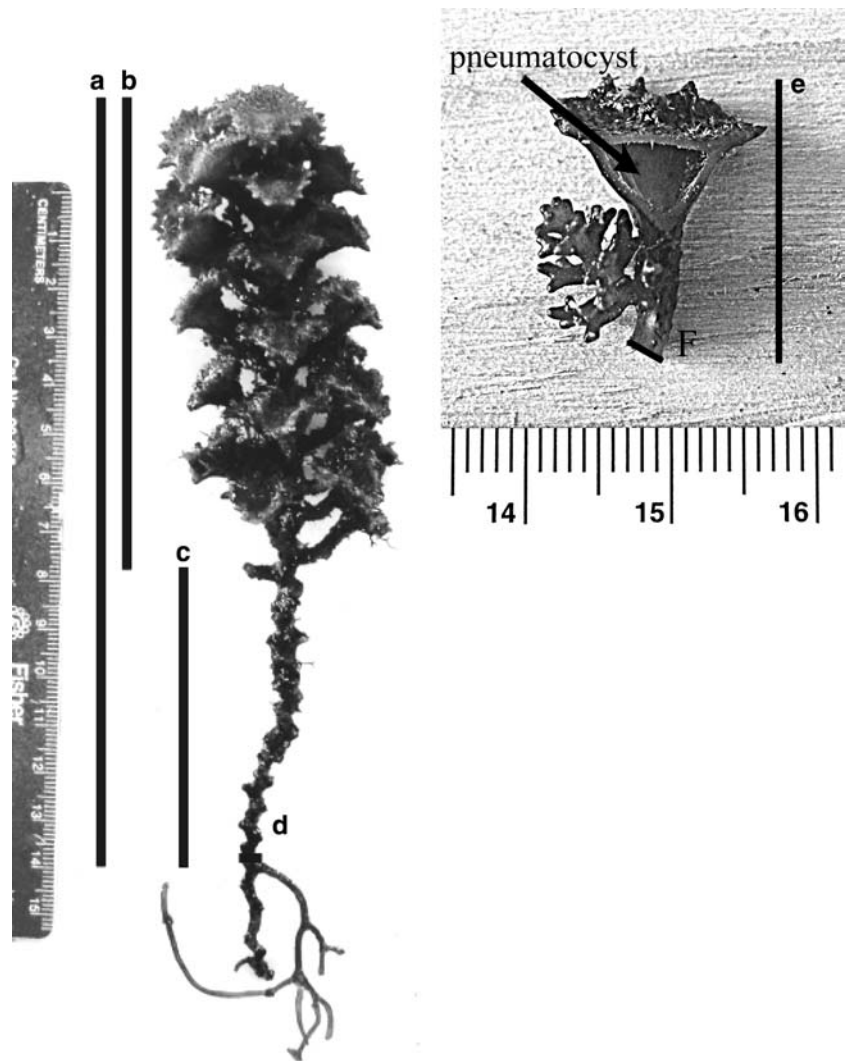
of ten fronds from the forereef and ten from the back-reef.

Material properties

Both the material properties of an organism's tissues and the organism's size and shape dictate how it deforms in response to an applied load such as hydrodynamic forces. Elastic modulus, extension ratio, and breaking stress of *T. ornata* stipes were measured by conducting tensile stress-extension tests on *T. ornata* stipes [as described by Koehl and Wainwright (1977)], using a tensometer constructed for field use. The stipes of *T. ornata* were used for these tests as this was where fronds broke when pulled experimentally from the substratum, and fronds found in floating mats were broken along the stipe.

One end of each stipe was clamped onto a stationary, machined aluminum beam. The other end of the stipe was clamped securely to a beam whose distance from the other beam could be altered by a hand-cranked lead screw. Stipes were wrapped in paper towel and neoprene and then clamped onto the end of the beam. Care was taken not to damage the tissue of the stipe as it was clamped, and any stipe that broke at or near the clamp was not used. The original length of the portion of the stipe between the clamps was measured to the nearest 0.1 mm with digital calipers. The length of the stipe as it was pulled was measured using a linear variable differential transformer (LVDT) (Pickering & Co. Model 7308-X2-AO, OH, USA) to the nearest 0.1 mm. The rate of extension was held constant by making one rotation of the lead screw crank each second. This produced an extension rate of 0.016/s. Voltages from the LVDT were recorded at 10 Hz and converted to digital signals using a data acquisition card (National instruments DAQ 1200), and recorded on Labview software (National Instruments, Version 3.0). Voltage changes were transformed to length measurements using calibration equations established by measuring the change in voltage for a known increase in length. The extension ratio (λ) is a measure of the extension of a material, and was calculated using the equation:

$$\lambda = (L - L_o)/L_o, \tag{1}$$

where L_o was the original length of the stipe being tested, and L was the length of the stipe as it was pulled. The extension ratio at the point at which the stipe broke is the breaking extension (λ_{BRK}) and is a measure of the material's extensibility.

The force with which the stipe resisted the extension was measured to the nearest 0.001 N using a strain gauge made of two 120-Ω resistors (Micro-Measurements Group Inc., type CEA-06-062UW-120, PA, USA) glued flush to either side of the stationary beam to which the stipe was attached. Voltages generated from the deformation of the strain gauges via a Wheatstone bridge were recorded using a bridge amplifier (Gould, model 11-4113-01) and the configuration described above. The force transducers were calibrated by hanging weights from a string attached to the beam at the same point that the stipes were attached. 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 beam. Weights of known masses were hung from the transducer. Each weight was hung three times and the mean of the voltages registered for each weight was multiplied by the acceleration due to gravity (9.81 m/s^2) to yield the force experienced by the strain gauges. A linear regression ($r^2 = 0.86$) was established from the linear relationship between voltage and force, with a precision of 0.001 N.

Stress (σ) for each stipe as it was pulled was calculated by:

$$\sigma = F/A, \tag{2}$$

where F was the force with which the specimen resisted an extension and A was the cross-sectional area. The breaking stress (σ_{BRK}) is the stress at which the specimen broke and is a measure of the strength of the tissue. Elastic modulus (E) of a material is a measure of its stiffness and was calculated for each stipe from the slope of plots of stress as a function of extension ratio.

Transplant experiments

Transplants of fronds from the forereef to the backreef, and from the backreef to the forereef were conducted during September–November, 2002. Fronds from the backreef and the forereef were randomly collected and held in running seawater in shaded tanks until transplanted. The length of each frond and whether it was positively or negatively buoyant was recorded prior to transplantation. Ten fronds from each habitat were transplanted to the other habitat, in addition to ten control fronds from each habitat that were transplanted back to their original habitat. Fronds were attached by their holdfasts with cable ties to chicken wire that had been wrapped around cement blocks that were fixed with Z-spar® underwater epoxy to the substratum in each habitat. After 8 weeks, fronds were collected and the length and proportion of blades with pneumatocysts was recorded. To determine the presence of pneumatocysts all blades were sliced longitudinally. A blade was considered to possess a pneumatocyst if it possessed a gap in the tissue in the center of the blade that exceeded 1 mm in diameter. The buoyant force (F_B) of all algae from the transplant was calculated using the equation:

$$F_B = gV(\rho_a - \rho_w), \tag{3}$$

where 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 seawater (1023 kg/m^3 at 25°C; Vogel 1994). Volumes of fronds were determined by measuring displacement of the volume of water in a graduated cylinder after a whole algal frond had been submerged into it. Dividing the mass of each frond by its volume yielded estimates of the density of each algal body, including associated pneumatocysts for backreef algae. The mass of each frond was determined from the mean of two measurements on an Ohaus Explorer precision balance to the nearest 0.01 g.

Drag coefficient

Algae can be exposed to unidirectional or wave-driven flow that results in bi-directional flow along the substratum. The forces experienced by an alga can include drag, acceleration reaction, and inertial. Peak drag forces occur at maximum velocities. Acceleration reaction is highest during high rates of change of velocity. Inertial forces occur when a flexible organism that is moving in the direction of the flow comes to the end of its tether and its mass is suddenly brought to a halt (Denny 1988). In this study I consider only drag forces because backreef fronds are exposed to unidirectional flow where drag forces dominate, and drag should be the dominant force acting on forereef organisms as waves pass (Denny 1995; Gaylord 2000). In the forereef, the displacement of the water in either direction under waves of 8–10 second period is much larger then the length of the algae and they are pulled in one direction and then the other for long periods of time. Work by Gaylord (2000) suggests that the spatial scale of wave-induced accelerations is too small to encompass any alga large enough to be at risk from accelerational force. Additionally, measurements of horizontal force experienced by fronds of T. ornata from both backreef and forereef locations in waves did not exhibit a substantial force at the time that water velocity approached 0 m/s (Stewart 2004), as would be indicative of inertial force (Denny et al. 1998).

Drag (f_d), the force pushing an organism downstream in moving fluid was calculated using the empirical equation:

$$f_d = 1/2\rho U^2 S_p C_d. \tag{4}$$

where ρ is the density of water (1,023 kg/m^3 at 25°C), U is the water velocity, S_p the planar surface area of the

object, and C_d is the drag coefficient, a function of the shape of the object. The surface area of each frond to 0.01 cm^2 was calculated using NIH image (v 1.61) by measuring its area from a digital picture of the frond on its side. An estimate of area was made for two photographs of each alga and the mean of these estimates was used. The drag forces on five fronds from the forereef and the backreef were recorded at a range of flow speeds from 0.32 to 0.75 m/s in unidirectional flow with a working section of $0.40{\times}0.40$ m^2 in cross-sectional dimensions and 2.33 m in length. Flow in the flume was created by a propeller with adjustable speed of rotation. Force measurements were made in the center of the flume where the algae were not affected by lateral boundary layers from the walls of the flume. Flow speeds were calibrated at mid water depth in the flume using an accoustic doppler velocimeter (Sontek/YSI Inc., CA, USA) and the flow was recorded just above each alga during drag measurements. The force experienced by each frond was measured by force transducers that were made according to the design in Koehl and Wainwright (1977) using the equipment described in Stewart (2004). The C_d at each flow speed was then calculated from Eq. (4).

Environmental stress factor

The ESF is the ratio of the breaking stress of the stipe at a particular stage in its ontogeny (calculated above) divided by the stress due to drag experienced by the frond in flow velocities experienced during that season in its habitat. I calculated the ESF for forereef and backreef algae for a range of velocities to explore the consequences of the frond morphology to the likelihood of detachment in different flow habitats. Stress experienced in the stipe of algal fronds due to drag was calculated by dividing the mean drag force experienced by forereef and backreef fronds (calculated above) by the mean cross-sectional area for forereef and backreef stipes for flow speeds of 0–12 m/s. The C_d values obtained at the highest flow speeds in the flume (0.6 for forereef algae and 0.5 for backreef algae) were used to calculate ESF at flow speeds faster than those possible in the flume.

Results

Flow in forereef and backreef

Flow on the forereef was faster than in the backreef over the same time period. Flow velocities in the backreef averaged 0.14 ± 0.06 m/s (mean $\pm$ SE), while maximum forereef flow velocities averaged 1.04 ± 0.26 m/s. These estimates were made on relatively calm days in winter (the calm season on the north side of Moorea), and therefore are not indications of the maximum velocities at these sites. These measurements are in no way attempts to characterize the complete flow environment of the two sites, however they do provide an example of the relative differences in flow velocities experienced on the forereef and in the backreef.

Morphometrics

The morphology of backreef and forereef fronds differed in many ways (Table 1). In particular, backreef fronds were longer (both unbladed and bladed regions), had more blades and thinner stipes. All blades of backreef fronds possessed pneumatocysts, whereas only few blades of forereef fronds contained pneumatocysts, and these were very small.

Material properties

The stipes of forereef fronds had higher breaking stress and breaking extension ratios than backreef fronds, and although forereef fronds showed a trend toward higher elastic moduli than backreef fronds, the difference was not statistically significant (Fig. 2).

Transplant experiment

Fronds transplanted from the backreef to the forereef were broken along the stipe and none remained at the end of the experiment, whereas a proportion of 0.7 of forereef fronds transplanted to the forereef survived the transplant and were present at the end of the 8-week

Table 1 Morphometrics of backreef and forereef thalli

Morphometric	Backreef	Forereef	P-value
Thallus length (cm)	18.8 ± 1.99	9.9 ± 0.83	< 0.05
Bladed length (cm)	11.5 ± 0.43	7.2 ± 0.47	< 0.05
Unbladed length (cm)	9.24 ± 0.56	2.68 ± 0.72	< 0.05
Thickness at holdfast (cm)	0.27 ± 0.022	0.32 ± 0.012	< 0.05
Blade length (cm)	1.60 ± 0.48	1.72 ± 0.39	< 0.05
Blade diameter at stipe (cm)	0.25 ± 0.08	0.32 ± 0.05	< 0.05
Distance between blades (cm)	1.06 ± 0.049	1.13 ± 0.067	0.42
# Total blades	39 ± 1.1	24 ± 1.8	< 0.05
% Blades with pneumatocysts	100 ± 0.00	4.03 ± 2.64	< 0.05

All comparisons are by t-tests (Mean $\pm$ SE, $n = 10$)
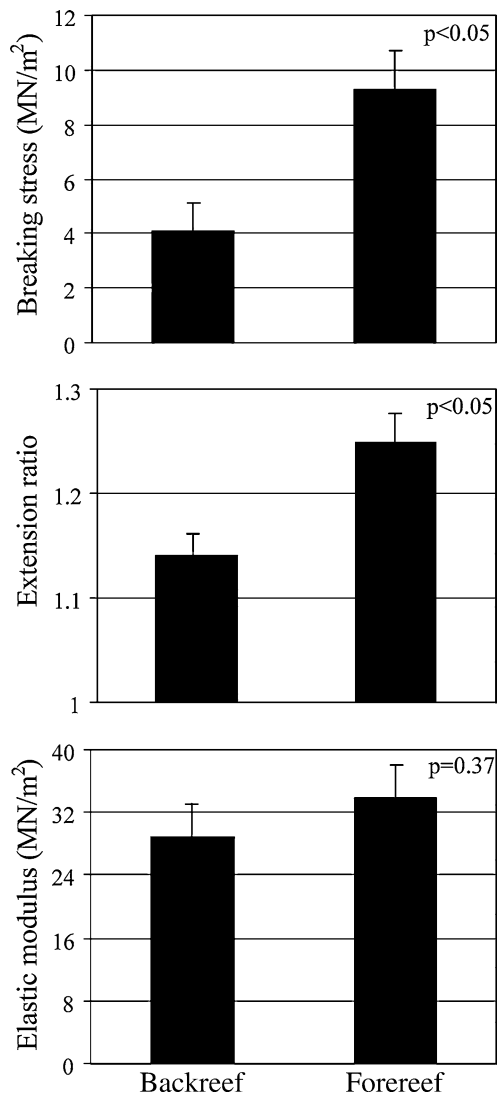
Fig. 2 Summary of material properties of backreef and forereef fronds from stress-extension tests. Breaking stress and breaking extension ratio were significantly higher for forereef fronds than backreef fronds as determined by t tests (stress: $t = 2.54$, df = 18, $P < 0.05$, extension ratio: $t = 1.97$, df = 18, $P < 0.05$) but differences in elastic moduli were not statistically different ($t = 0.92$, df = 18, $P = 0.37$)

period. A proportion of 0.9 of both the forereef fronds transplanted to the backreef and the control backreef fronds survived the transplant (Table 2).

At the end of the transplant, fronds transplanted from the forereef to the backreef had developed pneumatocysts in their blades, while controls transplanted back to the forereef had not. Of the ten fronds transplanted from the forereef to the backreef, seven floated, and two did not. Of the floating transplanted fronds, 0.70 ± 0.02 of their blades developed pneumatocysts over the course of the transplant. The two fronds that did not float developed pneumatocysts in 0.4 ± 0.1 of their blades, but still experienced negative buoyant forces. This is compared to 0.001 ± 0.0005 of blades that contain pneumatocysts of forereef fronds transplanted back

to the forereef, and 0.87 ± 0.05 of backreef fronds transplanted back to the backreef that contain pneumatocysts (Fig. 3).

Drag coefficient

The drag coefficient was higher for forereef fronds than backreef fronds at low flow speeds (0.32 and 0.5 m/s), but the difference decreased at higher flow speeds (Fig. 4a). Forereef fronds were not realigned in the direction of flow to the same extent as backreef fronds when both were exposed to similar flow speeds. The more upright posture of forereef fronds at low flow speeds correlated with higher values of C_D. At high flow speeds, the forereef fronds were bent over in the flow to a similar extent as backreef fronds and the C_D approached that of the backreef fronds.

Environmental stress factor

The ESF was higher for forereef fronds than backreef fronds at all flow speeds from 0 to 6 m/s (Fig. 4b). At flow speeds typical of estimates of flow speeds in the backreef on calm days (< 1 m/s) the ESF is high ($+2.5$) for both backreef and forereef fronds, suggesting that on calm days it is unlikely that fronds of either morphology would be swept away by ambient water motion in the backreef. The ESF drops below one for backreef fronds at 1.7 m/s, and at 4.2 m/s for forereef fronds.

Discussion

Buoyancy of *T. ornata*

Data from the transplant experiment suggest that the production of pneumatocysts and corresponding increase in buoyant force is a plastic trait that is influenced by flow environment. Buoyant fronds of *T. ornata* disperse by drifting, with fertile fronds capable of dispersing 100s of km on ocean currents before releasing germlings (Stiger and Payri 1999b). Plasticity in the ability to produce pneumatocysts ensures that new populations of *T. ornata* in calm habitats can produce buoyant fronds, which can in turn, disperse by drifting. This has proven to be a successful dispersal strategy for *T. ornata* in, that has been attributed to its increase in

**Table 2** Proportion survival of transplanted thalli (n = 10 for all treatments)

Treatment	Proportion survived
Forereef → Forereef	0.70
Forereef → Backreef	0.90
Backreef → Backreef	0.90
Backreef → Forereef	0
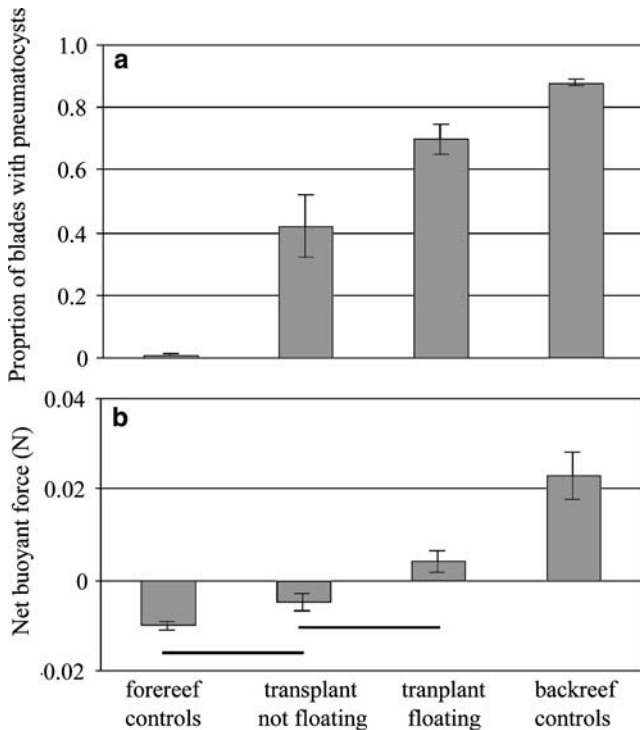
Fig. 3 Results of 8-week-transplant experiment for forereef fronds transplanted to the backreef. "Forereef controls" are forereef fronds returned back to the forereef for the transplant experiment ($n=7$). "Transplant—not floating" are fronds transplanted from the forereef to the backreef that were not floating at the end of the experiment ($n=2$). "Transplant floating" are forereef fronds transplanted from the forereef to the backreef that were floating at the end of the experiment ($n=7$), and control backreef fronds ($n=9$) are backreef fronds returned to the backreef for the transplant experiment. None of the backreef fronds transplanted to the forereef survived the transplant. **a** The proportion of blades that contained pneumatocysts were significantly different between all groups as determined by a Kruskall–Wallis test ($H=26.43$, df $=3$, $P<0.001$) and non-parametric post-hoc pair-wise comparisons (Zar 1999). **b** Buoyant force was similar for forereef controls and non-floating transplants, and for non-floating transplants and floating transplants, but was higher for backreef controls as determined by a Kruskall–Wallis test ($H=12.60$, df $=3$, $P<0.05$). The bar under data of different treatments indicates non-significant differences as determined by non-parametric post-hoc pair-wise comparisons.

abundance and distribution across islands throughout French Polynesia (Payri and Naim 1982; Stiger and Payri 1999b).

Changes to size and shape of existing pneumatocysts associated with environment have been reported for a number of algae. More streamlined shapes and smaller size of pneumatocysts have been reported to correlate with high flow areas in other algae (Brandt 1923; Druehl 1978; Pace 1972; Dromgoole 1981; Norton et al. 1981) suggestive of a drag-reducing response in high flow. The effects of pneumatocysts in altering drag in this study are confounded by the other morphological differences between forereef and backreef algae. However, Stewart (2004) did find that backreef fronds experimentally manipulated to be non-buoyant (while maintaining all other morphological variables) experienced higher
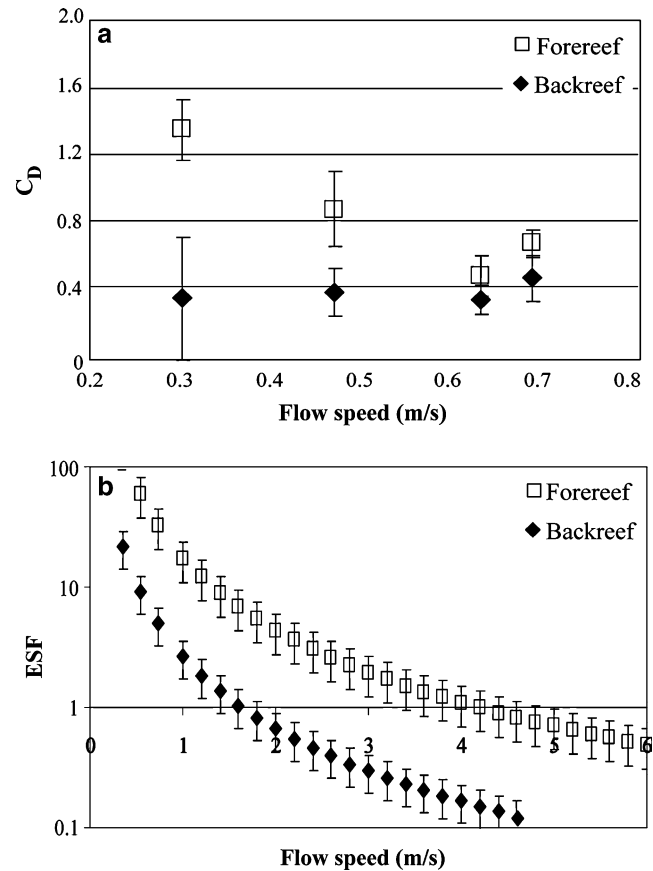
Fig. 4 a Drag coefficient (C_D) of backreef and forereef fronds at flow speeds from 0.32–0.75 m/s (Mean $\pm$ SE, $n=5$). C_D is higher for forereef fronds at 0.34 m/s (Mann–Whitney U, $z=-1.98$, $P<0.05$) and at 0.5 m/s ($z=-1.99$, $P<0.05$), but not at 0.67 m/s ($z=-1.78$, $P=0.076$) or 0.75 m/s ($z=-1.57$, $P=0.12$). **b** Environmental stress factor (ESF) of backreef and forereef fronds at unidirectional flow velocities from 0–6 m/s. For extrapolations beyond 0.75 m/s, the C_D determined at the highest flow speed (0.75 m.s) was used in ESF calculations.

horizontal force in moving water than buoyant backreef fronds. Therefore, the absence of pneumatocysts in forereef frond suggests that this is a drag-reducing mechanism. Production of pneumatocysts in low flow suggests that there are advantages to buoyancy when not overshadowed by disadvantages due to hydrodynamic forces in high flow.

It is not clear how expensive, in terms of resources, buoyancy is to produce and maintain in *Turbinaria* or algae in general. Production of gas-filled pneumatocysts may be a less energetically expensive mechanism of imparting buoyancy than other mechanisms such as oil bodies and ionic regulation (Walsby 1972), but allocation of resources away from blades to air bladders and fertile tissue may result in decreased photosynthetic performance (Kilar et al. 1989). Buoyancy in *T. ornata* provides a mechanism to maintain backreef fronds in an upright position, which for forereef fronds is accomplished by thick, short stipes, and high flexural stiffness (Stewart 2004). But, its not clear if and to what extent the combination of low tissue strength and high buoyancy,

or low buoyancy and high strength might be the result of resource allocation.

Morphological differences

Aspects of the morphology of *T. ornata* from each habitat may contribute to the differences in drag coefficients for these fronds. Increased length of backreef fronds likely contributed to their higher drag coefficients than shorter forereef fronds at low velocities. However, the low flexural stiffness of the stipes of backreef fronds (Stewart 2004) allowed them to bend over toward the substratum where they experienced reduced velocities and force lower in the benthic boundary layer as flow speed increased. Short forereef fronds may find some refuge from high forces lower in the boundary layer on the forereef, but their high breaking stress allows them to cope in this high flow environment. Forereef fronds were thicker in their stipes and at the attachments of blades to the stipe, making them overall more robust than backreef fronds.

The elastic modulus was not statistically significantly different for backreef and forereef fronds indicating that forereef and backreef fronds are stretchy to the same degree. Forereef fronds had higher breaking extension ratios and higher breaking stress than backreef fronds indicating that forereef fronds must be pulled to longer extensions to cause them to break and that they experience higher stress to pull them to such extensions. Because the stipes of forereef fronds are thicker than backreef fronds at the point at which they break (Table 1), the higher breaking stress of forereef fronds is indicative of stronger fronds, as more force is required to break forereef fronds than backreef fronds.

Drag coefficient

The morphological variation between forereef and backreef fronds results in higher drag coefficients for forereef fronds than backreef fronds at low flow speeds. However, these differences are reduced as flow speeds increase (Fig. 4a). Due to the non-predictable relationship between drag coefficient (C_D) and flow speed (Vogel 1994), the estimates of C_D are limited to the maximum velocity of the flow tank (0.75 m/s). Extrapolations to higher flow speeds can be unreliable, as algae with strap-like or pliable blades are moved into increasingly streamlined shapes by increasing water velocities (Sheath and Hambrook 1988; Carrington 1990; Stewart and Carpenter 2003) decreasing the forces they experience (e.g. Carrington 1990). However, the unique pine-cone-like shape of *T. ornata* makes it behavior in moving water unlike that of many other macroalgae. The blades of *T. ornata* do not reorient relative to the stipe, and the frond does not take on a new overall shape, but retains its pine-cone like shape even at the highest flow velocities. Yet, at high velocities whole fronds of backreef

T. ornata were pushed toward the substratum and may experience slower flow lower in the boundary layer at high flow speeds.

Environmental stress factor

The results of this study suggest that fronds of *T. ornata* from the backreef and the forereef are well suited for their respective habitats, at least with respect to potential for dislodgment due to drag. Based on ESF values, backreef fronds are expected to break at lower velocities than forereef fronds (Fig. 4b). Maximum instantaneous flow velocities in the backreef during storms can reach 1.0–2.0 m/s (J. Hench personal communication), and the ESF at which adult backreef fronds are expected to break (1.6) falls within this range. A rough estimate of horizontal maximum velocities (u_{max}) for submerged organisms under breaking waves can be calculated using:

$$u = 0.3\sqrt{g(h + d)},$$

where g is the acceleration due to gravity (9.81 m/s^2), h the breaking wave height, and d is the depth of water under the breaking wave (Denny 1995). Based on estimates of the maximum height of breaking waves on the north shore of Tahiti (http://polar.wwb.noaa.gov/waves/locations), h can range from 4-15 m during storms. At depths of 1–10 m, water velocities under these waves can range from 2.3-4.7 m/s. The ESF for forereef fronds reaches one (indicating that fronds will break) at 4.3 m/s. Therefore, adult forereef fronds are expected to break under big waves in storms. However, during more moderate weather h ranges from 1-3 m, leading to velocities under these waves of 1.9–3.3 m/s and forereef fronds are not expected to break under these conditions. Wave heights of approximately 2.0 m occurred during a storm in the course of the transplant experiment. Experimental fronds were located at 3-meter depth on the forereef. Backreef fronds, which had been transplanted to the forereef did not survive this storm but forereef fronds did. Calculated ESF for transplanted backreef fronds under such waves is less than one, confirming that the stress experienced by backreef fronds under these storm conditions was greater than their breaking strength. Therefore, despite the considerable differences in the flow environments, and morphological differences in the fronds of *T. ornata* in each habitat, the likelihood of breakage is similar for backreef fronds and forereef fronds in their respective habitats. Under normal non-storm conditions, both backreef and forereef fronds are not expected to break. However, during storms, ESF calculations predicts that both backreef and forereef fronds will break. Indeed, large mats of floating fronds are present in backreefs followings storms in Moorea (personal observation), and although more difficult to observe because they sink, one can observe groups of detached non-buoyant fronds on the substratum on the forereef after large waves.

The ESF calculated here are based on measurements of drag, and it is possible that the oscillatory nature of the flow on the forereef introduces acceleration reaction forces that may play a role in dislodgement of these fronds. Acceleration reaction was not considered here, in part for the reasons in noted in the *Drag coefficient* section of the methods. However, it is acknowledged that other forces than drag may be affecting the survival of *T. ornata* in the forereef, and perhaps in the backreef as well during big storms backreef fronds may be exposed to waves that pass over the crest. Drag is certainly a predominant force in both habitats and for this reason estimates of ESF were calculated using drag. However, estimates of ESF for forereef fronds may overestimate the ability of forereef fronds, and perhaps backreef fronds to persist during big storms. A similar approach was taken by (Pratt and Johnson 2002) to determine the ESF for algae exposed to different intertidal wave exposures.

The ESF described above were based on measurements made on healthy adult fronds. The ESF of fronds of backreef *T. ornata* decreases with age (Stewart *in press*), with older fronds facing increased risk of detachment than younger fronds. Rafts of *T. ornata* found floating after storms are composed mostly of mature, old fronds, which have lower breaking stresses than adult fronds (Stewart 2006). This pattern of lower strength and lower ESF for old fronds than young fronds has also been shown for another buoyant alga, the giant kelp *Nereocystis luetkeana* (Johnson and Koehl 1994). As noted above, dislodgement of buoyant *T. ornata* fronds is an important dispersal mechanism, and so cannot always be considered detrimental to the survival of a frond.

Advantages of site-specific morphologies of fronds of *T. ornata*

Aspects of the morphology of fronds typical of the backreef and the forereef may confer advantages specific to their habitats. Because *T. ornata* needs hard substrate for attachment, attachment of backreef algae is limited to patches of dead coral on bommies separated by sand. Since settlement space is limited on these small patches, dense aggregations of *T. ornata* occur on such patches, and competition for light interception may arise between fronds. Long, buoyant fronds that protrude to the tops of aggregations are not shaded as severely as short ones (Stewart unpublished data), and frond length and buoyancy increase light interception within aggregations. As backreef fronds experience relatively low water motion, damage by hydrodynamic forces may be less of a concern for these algae than light interception. In addition, flow velocities may be reduced inside aggregations of *T. ornata* (Stewart unpublished data), as has been shown in kelp forests (e.g. Eckman 1987, 1989; Jackson 1997) and seagrass (e.g. Fonseca et al. 1983). Reduction of flow in algal assemblages can reduce the force that fronds experience within the assemblage (Johnson 2001), further reducing the chance of breakage of backreef fronds.

Forereef fronds of *T. ornata* are one of few organisms (in addition to encrusting coralline algae and some corals) that are able to persist under breaking waves on the forereef. The substratum in this region is composed primarily of coral pavement, and *T. ornata* is a dominant organism in this habitat. This is perhaps one of few places on a coral reef that there is not intense competition for space or light, and fronds of *T. ornata* do not grow in dense aggregations on the forereef, but spread out over the substratum. Therefore, the morphology of forereef algae may be shaped more by hydrodynamic force than are backreef algae, and the shape and material properties of forereef algae of *T. ornata*, particularly its strength, has enabled it to persist in this habitat.

Conclusions

This study has shown that aspects of morphology differ between backreef and forereef habitats, and that one aspect of morphology of *T. ornata*, the production of pneumatocysts and resulting buoyancy is a phenotypically plastic trait in response to water motion. Forereef algae are stiff, negatively buoyant, strong, and experience high drag forces, and backreef algae are buoyant and weak. Yet, the morphology of backreef and forereef fronds confers advantages to survival in their respective habitats, and the chance of detachment may be similar for forereef and backreef fronds.

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