

Habitat-induced morphological variation influences photosynthesis and drag on the marine macroalga *Pachydictyon coriaceum*

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Abstract Photosynthesis, growth, distribution, and persistence of macroalgae are determined in part by the physical environment in which they live. Therefore, discerning how macroalgae interact with their physical environment is necessary to better understand their physiological performance. The purpose of this study was to examine what photosynthetic and hydrodynamic costs and benefits the morphology of *Pachydictyon coriaceum* (Phaeophyta) confers on the thallus in a given environment. Principal components analysis of morphometric measurements of *Pachydictyon coriaceum* from different flow habitats and depths separated thalli into three distinct morphs: shallow wave-exposed, shallow wave-protected, and deep. To test the hypothesis that thallus morphology affects net photosynthesis (NP), thalli of three morphotypes of *P. coriaceum* were incubated in an enclosed recirculating flume under three simulated light/water flow environments representing conditions from which the three morphotypes were collected. The wave-protected and deep morphs had significantly higher rates of photosynthesis than the wave-exposed morph for all three

simulated environments. The dense, compact shape of the wave-exposed morph readily streamlines with flow and in doing so, potentially shades many of its internal blades likely accounting for its lower biomass-specific NP. Drag coefficients (C_d) were estimated for the three morphotypes over a range of flow velocities between 0.08 and 0.47 m s⁻¹. At lower water flow velocities (0.08–0.21 m s⁻¹), wave-exposed morphs had the lowest C_d among the three morphotypes. But drag coefficients of the three morphotypes converged with increasing flow velocities, and at velocities >0.31 m s⁻¹ there were no differences in C_d among the three morphotypes. The results of this study indicate that the environmentally-shaped morphs influence photosynthesis and, to a lesser degree, hydrodynamic forces acting on *P. coriaceum*.

Introduction

The morphology of an organism impacts its performance in a given environment which, in turn, determines its ecological success (Koehl 1996). Many marine organisms have morphologies that reflect their physical environment. Some of the best examples of morphological variation in marine organisms with respect to physical forces come from studies of benthic macroalgae which have been shown to display varying morphologies depending on the water flow environment in which they live (de Paula and Oliveria 1982; Druehl and Kemp 1982; Sideman and Mathieson 1985; Gerard 1987; Koehl and Alberte 1988; Jackelman and Bolton 1990; Gutierrez and Fernandez 1992; Collado-Vides and Robledo 1999). Macroalgal thalli growing in wave-protected sites often have ruffled or undulate

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blades (Koehl and Alberte 1988; Armstrong 1989; Johnson and Koehl 1994; Hurd et al. 1996) compared to those found in wave-exposed habitats. Macroalgae from wave-exposed habitats generally are smaller (Carrington 1990; Blanchette 1997), have narrower, thicker and smoother blades (Gerard and Mann 1979; Hurd et al. 1996; Kawamata 2001), and branch more (Gutierrez and Fernandez 1992) compared to those from wave-protected habitats. These morphological characteristics have been shown to mitigate hydrodynamic stresses like drag or dislodgment (Koehl and Alberte 1988; Armstrong 1989; Carrington 1990; Dudgeon and Johnson 1992; Johnson and Koehl 1994; Kawamata 2001) and reduce turbulence (Anderson and Charters 1982).

For photosynthetic marine organisms, light limitation is another important physical stress that can affect morphology. Shading experiments on a marine angiosperm by Goldsborough and Kemp (1988), revealed that a species of aquatic plant, *Potamogeton perfoliatus* L., can change its morphology in response to light attenuation. Gerard (1988) found that blades of *Laminaria saccharina* from deeper water were thinner compared to those from shallow depths. Further, thinner blades have been shown to be more photosynthetically efficient than thicker blades (King and Schramm 1976; Lüning and Dring 1985; Nielsen and Sand-Jensen 1990; Gerard 1988; Peckol and Ramus 1988; Enriquez et al. 1995; Johansson and Snoeijs 2002). Hay (1986) proposed that in habitats where light is limited, monolayered thalli should be dominant and in high light habitats, multilayered morphs should be more abundant. However, Peckol and Ramus (1988) found that multilayered species dominate in deep water habitats off Cape Fear, NC, USA. Still, the effects of light attenuation on macroalgal morphology remain ambiguous.

The effects of light and water flow on macroalgae occur at the surface of the thallus so morphology plays an important role in optimizing photosynthetic production and growth. Water flow can reconfigure thallus morphology affecting their photosynthetic properties. For example, in low flow habitats, seaweeds with blades that are broader and ruffled can reorient in slow currents (10 cm s^{-1}), spreading out perpendicular to incident light, and possibly facilitating photon capture (Hurd et al. 1997). However, at higher flow velocities thallus reconfiguration can result in increased self-shading and a decrease in net photosynthesis (Stewart and Carpenter 2003). Gerard and Mann (1979) found that the wave-protected morph of *Laminaria longicruris* facilitated light capture and mass transfer of nutrients.

Macroalgal morphology also has been shown to reduce the effects of mechanical stresses caused by water motion. For example, flow-influenced changes in algal morphology can reduce the probability of dislodgment from the substratum (Carrington 1990; Hawes and Smith 1995; Shaughnessy et al. 1996; Blanchette 1997; Kawamata 2001; Blanchette et al. 2002). Armstrong (1989) showed that the strap-like bladed, wave-exposed morph of *Hedophyllum sessile* (Phaeophyceae) experienced less drag than the bullate bladed wave-protected morph at a given flow speed. Johnson and Koehl (1994) found similar results with *Nereocystis luetkeana* thalli from current swept sites versus those from wave-protected sites. However, Milligan and DeWreede (2004) concluded that for *H. sessile*, size, not shape was the most important determinant of drag force experienced by the thallus.

In habitats where water flow is high, a highly-branched morphology may dampen turbulence (Andersen and Charters 1982) thereby reducing hydrodynamic drag. Thallus size also has been shown to be important to the survival of intertidal organisms (Denny et al. 1985; Gaylord et al. 1994; Blanchette 1997). Thus, smaller thalli with narrow blades, thicker stipes, or an overall compact morphology may withstand higher flow velocities than more delicate, foliose forms. Manipulative experiments conducted in situ by Stewart and Carpenter (2003) demonstrated wave-induced morphological plasticity in two species of Dictyotales. Thalli experimentally protected from water flow had longer and wider blades than those exposed to water motion. However, Carrington (1990) measured drag on intertidal seaweeds of varying sizes and morphologies and found that their drag coefficients converged as water velocity increased, suggesting that morphology may be less important to drag mitigation at higher flow speeds (i.e., $3\text{--}4 \text{ m s}^{-1}$).

The idea that for any macroalgal morphology there is a trade-off between photosynthetic performance and hydrodynamic stress mitigation has been presented previously (Gerard and Mann 1979; Littler and Littler 1980; Koehl 1986; Koehl and Alberte 1988; Kübler and Dudgeon 1996). An alga can allocate photosynthate to structural components to withstand forces associated with water motion, photosynthetic tissue to capture light energy, and reproductive tissue. In environments where carbon is limiting either due to low light or to mass transfer limitations, allocation of photosynthate to one component limits the amount available to another. Further, allocation to one component can be detrimental to another. For example, a thallus with thick blades may be able to withstand greater drag forces but at a cost of increased internal self shading.

Or, a thallus with broad blades may be able to capture light more efficiently at the cost of increasing drag that can cause thallus damage or dislodgment.

The branched, bladed alga, *Pachydictyon coriaceum* (Class Phaeophyceae, Order Dictyotales) grows from the lower intertidal to depths of about 13 m (Abbott and Hollenberg 1976) and is found commonly in the understory of kelp forests at Santa Catalina island, CA, USA. *Pachydictyon coriaceum* is perennial, persisting in both wave-exposed and wave-protected habitats where it exhibits strikingly different morphologies (Fig. 1). This study examined the relationship between thallus morphology, photosynthetic performance, and mitigation of drag forces. Experiments were designed to identify different morphologies of *P. coriaceum* and then address whether these morphotypes exhibit different rates of photosynthesis and/or experience different magnitudes of drag.

Materials and methods

The study was conducted at Santa Catalina Island, CA, USA, near the Wrigley Marine Science Center (WMSC, 118°27' W 33°42' N) where the surrounding nearshore environment provided habitats with varying light and flow regimes. Four sites were chosen (Fig. 2); the NW sides of Bird Rock and Isthmus Reef served as wave-exposed sites as they are unprotected from the prevailing NW swell and Blue Cavern and the Quarry, nearby coves, were chosen as wave-protected sites. Thalli were collected from two depths at each site, 2 and 10 m, returned to the laboratory, and placed in running seawater. Experiments were conducted within 24 h of collection. Morphometric analyses were conducted in fall 1999. Photosynthesis experiments were

conducted in fall 2000. Drag experiments were conducted in spring 2002.

Light measurements

Relative light availability was quantified at each site by measuring photon flux density (PFD, $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) in situ. Light measurements were made at all sites on two consecutive sunny days at or within 1 h of noon in July 1999 using a cosine-corrected Li-Cor light probe (Li-Cor Inc. Lincoln, NE). Three, 5-min measurements were taken at 2 and 10 m. Differences in PFD were analyzed with a two-way, Model I ANOVA with site and depth as factors.

Wave exposure

In June 1999, relative water flow at each site was estimated by measuring the dissolution of 12 plaster of paris blocks (clod cards) placed at 2 and 10 m at each site for 48 h (Doty 1971; Thompson and Glenn 1994). In January 2000, attenuation of water flow with depth at the wave-exposed and wave-protected sites was measured using gypsum blocks ($n = 10$) left in the water for 10 days. In October 2000, three maximum wave force dynamometers (sensu Bell and Denny 1994) were placed in shallow water (2 m) at exposed and protected sites for 10 days to quantify maximum flow velocities. Dynamometers were reset every other day during the 10 days to improve resolution. Differences in dissolution of plaster blocks were analyzed with a two-way, Model I ANOVA with site and depth as factors. Differences in dissolution of gypsum blocks

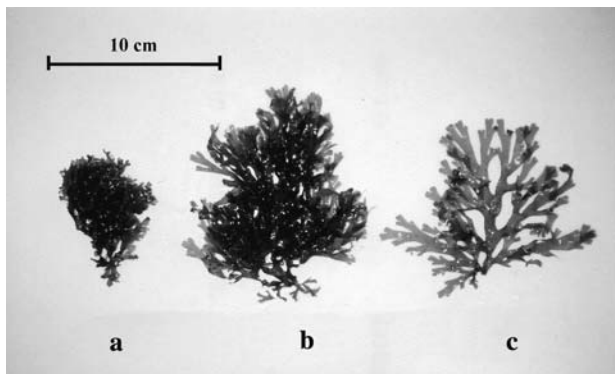


Fig. 1 *Pachydictyon coriaceum* morphotypes collected from **a** Bird Rock 2 m (wave-exposed), **b** Blue Cavern 2 m (wave-protected), and **c** the Quarry 10 m (deep)

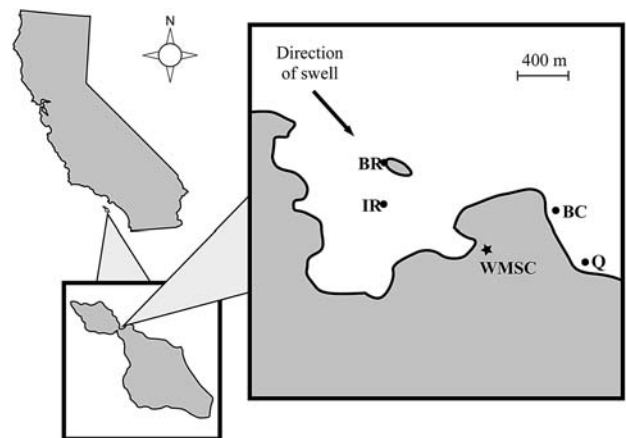


Fig. 2 Map of wave-exposed and wave-protected sites at Santa Catalina Island, CA, USA. The wave-exposed sites are: BR, Bird Rock and IR, Isthmus Reef. The wave-protected sites are: BC, Blue Cavern and Q, the Quarry

for both exposed and protected sites were analyzed with a Model I ANOVA with depth as the main factor. Differences in dynamometer measurements between exposure sites were analyzed with a Student's *t* test.

Relative abundance of *Pachydictyon coriaceum*

In June 2000, the percent cover and relative abundance of *Pachydictyon coriaceum* was estimated in 30-randomly-placed 0.25 m² quadrats at each wave-exposed and wave-protected site at both 2 and 10-m depths. In each quadrat we counted the number of thalli, estimated percent cover of *P. coriaceum* over the substratum, and estimated the degree to which each thallus was proliferated. To estimate thallus proliferation, individuals were scored on a scale ranging from 0 to 5 with 0 indicating no proliferative growth present and five indicating all terminal blades on the thalli showed signs of adventitious growth. The mean index per quadrat was calculated to give an overall estimation of thalli with proliferative growth per quadrat. Abundance, percent cover, and thallus proliferation index data were compared between wave-exposed and wave-protected sites for both depths. Abundance and percent cover data were analyzed using two-way ANOVAs with wave exposure and depth as factors. The thallus proliferation index was analyzed as rank sum data using a Mann–Whitney *U* test with wave exposure as the main factor.

Morphometrics

To characterize the overall morphology of *Pachydictyon coriaceum*, thalli were collected haphazardly from high and low flow sites at shallow (2 m) and deep (10 m) depths, taken to the lab, and measured. Each thallus was placed in individual re-closeable plastic bags. Excess water and air was removed from the bags and the thalli were frozen until morphometric measurements were conducted in the laboratory (<14 days). Ten thalli from each depth at each site were chosen at random for morphometric analyses and surface area/volume (SA:V) measurements. Overall thallus morphology from each environment was characterized by a suite of morphometric variables (Fig. 3): widest width of blades (WW), narrowest width of blades (NW), length between branches (LBB), blade thickness (BT), and proportion of terminal blades with proliferations (BP). Five blades per thallus were selected haphazardly and measured for each variable except for blade proliferation, for which the proportion of all terminal blades with proliferations was calcu-

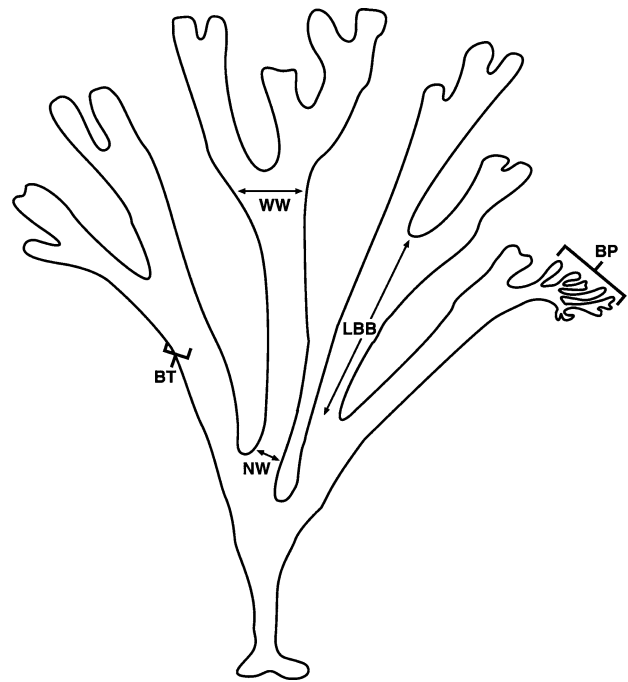


Fig. 3 Illustration of measurements used to characterize morphotypes. Measurements used for analyses were: widest blade width (WW), narrowest blade width (NW), length of blade between branches (LBB), blade proliferations (BP), and blade thickness (BT)

lated. Means per thallus for each variable were used as statistical replicates.

After morphometric data were collected, thallus surface area and volume were estimated. Thalli were picked clean of epibionts and spun in a salad spinner to remove excess water. Thallus volume was estimated to the nearest 0.1 ml by measuring their displacement of seawater in a graduated cylinder. Once volume was estimated, the thalli again were spun to remove excess water and their surface area was estimated using a dye-dipping technique modified from Hoegh-Guldberg (1988) and Stewart and Carpenter (2003). To account for allometric scaling, volume data were cube-root transformed and SA data were square root transformed before ratios were calculated. This created a unitless ratio that allowed a linear comparison of the two measurements with regard to shape but not size. Blade measurement data were log-transformed and proliferation data were arcsine-transformed prior to statistical analyses.

Principal components analysis was performed on morphometric and SA:V data to reduce morphometric variables into fewer principal components that could be used to define morphs from each environment. Interpretation of the loading matrix was facilitated by varimax rotation and only loadings greater than 0.32

were interpreted (Tabachnick and Fidell 1996). The resulting principal components were analyzed using MANOVA to determine if the component loadings differed among morphotypes. Data on SA:V also were analyzed using ANCOVA to determine how surface area scaled with volume for thalli growing in habitats differing in light and wave exposure. Individual morphometric variables were compared at each depth using Model I ANOVA with exposure as the main factor.

Photosynthesis experiments

Net photosynthesis (NP) experiments were conducted in the laboratory using an enclosed 28-l oscillating flume with a 10 cm × 10 cm × 110 cm working section. Rates of photosynthesis of three morphotypes of *Pachydictyon coriaceum* were estimated from changes in oxygen concentration (recorded each minute) over 15 min incubations using an oxygen meter (Nester Instruments). The flume was filled with filtered seawater and kept at a temperature of 17–20°C. Initial dissolved oxygen concentrations were reduced to levels approximately 20% below saturation before each incubation by sparging with nitrogen gas, and excess air bubbles were removed from the flume before sealing. Seawater was changed after every two incubations. Individual thalli were placed in the flume, and affixed in the center of the working section at the base of the stipe, near the holdfast using a small cable tie threaded through rubber tubing to prevent stipe damage. Light was provided from a 400-W metal halide bulb positioned over the working section of the flume. The amount of light received by each thallus was controlled by adding or subtracting layers of fiberglass window screening between the light source and the flume. For dark incubations used to estimate respiration, a canvas cover was placed over the flume to block out all light. PFD of photosynthetically active radiation (PAR, 400–700 nm) was measured in the flume using a Li-Cor quantum light meter with a 2π sensor.

To insure photosynthesis experiments were conducted at saturating light levels, minimum saturating PFDs were established for each morphotype. To determine photosynthetic parameters for the three morphotypes, NP versus PFD was measured. Three thalli of each morphotype were incubated individually in the flume for 15 min with a 10 s oscillating flow at a speed of 9.5 cm s⁻¹. NP was measured at six light levels between 0 and 1,000 μmol photons s⁻¹ m⁻². After incubations, thalli were dried at 60°C overnight, weighed, and NP was normalized to dry mass.

P_{\max} (maximum photosynthetic rate), I_k (minimum saturation PFD), and α (initial photosynthetic slope) were estimated after fitting a hyperbolic tangent curve to a plot of NP versus PFD (Jassby and Platt 1976).

To test the hypothesis that NP is dependent on thallus morphology, individual thalli of each morphotype were incubated in the flume under three simulated light/water flow environments: high flow/high light (21 cm s⁻¹, 1,000 μmol photons s⁻¹ m⁻²), low flow/high light (9.5 cm s⁻¹, 1,000 μmol photons s⁻¹ m⁻²), and low flow/low light (6.1 cm s⁻¹, 332 μmol photons s⁻¹ m⁻²). All morphotypes were saturated at 332 μmol photons s⁻¹ m⁻² (see Results).

Eight randomly-chosen thalli were incubated under each of the three flow/light combinations. NP was compared using a two-way model I ANOVA with morphotype and simulated environment as factors. The interaction between morphotype and simulated environment also was tested to determine if a morphotype performs best when exposed to light and flow conditions similar to the habitat from which it was collected.

Drag experiments

Drag was estimated on the three morphotypes at five unidirectional flow velocities (8, 16, 31, 39, 48 cm s⁻¹) in an 800-l recirculating flume with a 29 cm × 36 cm × 300 cm working section. Flow velocities in the flume were measured with a Marsh-McBirney electromagnetic flow probe (5-cm diameter) prior to the experiment. Seawater in the flume was made by adding Coralife® synthetic sea salt to fresh water and the temperature was regulated to 17–20°C with a refrigeration unit.

Thalli ($n = 10$) were collected haphazardly from sites representing the three light/flow regimes used in the photosynthesis experiments, returned to the laboratory, and kept in running seawater until used for drag experiments (<24 h). Drag forces were measured by using a force transducer modified from a digital scale (Mettler Toledo). Thalli were attached at the base of the stipe to a 1-cm lever in the center of the working section using a plastic cable tie. The lever was attached to a thin line which ran parallel to the floor of the working section then threaded through an eyebolt 20 cm downstream and up to the bottom weighing mechanism of the digital scale. The lever transduced the drag to a weight which was converted to force by multiplying by the acceleration due to gravity. Drag from the lever and line (without an algal thallus) were subtracted from the total drag value for each measurement.

Drag coefficients for each morphotype were calculated from the drag equation:

$$C_d = 2F_d/(\rho Au^2),$$

where F_d is the measured drag force, ρ density of seawater, A characteristic area of the thallus (maximal projected area), and u^2 squared water velocity. The characteristic area, A , was estimated from digital photographs of the thalli pressed under a clear acrylic plate with a ruler placed in the frame for calibration. Thallus area and length of the digitized images were calculated using image analysis software (NIH Image 1.62).

For flexible objects like macroalgae, the coefficient of drag decreases with increasing flow speed due to reconfiguration and compaction of the thallus, making it more streamlined in faster flow (Vogel 1984). To estimate the degree to which each morph reconfigured with an increase in flow speed, the Vogel number E was calculated (Vogel 1984). E is the exponent to which velocity must be raised to be proportional to speed-specific drag:

$$C_d \propto u^E.$$

A negative exponent indicates C_d decreases with increasing velocity and the value of the exponent indicates the magnitude to which the thallus has reconfigured from its original shape.

Results

Light attenuation

Anecdotal observations over the 24-month study suggested that light levels did not vary widely among sites. Light measurements (July 1999) support those observations although daily and seasonal light fluctuations were not measured. Mean photon flux density was not significantly different among the four sites (ANOVA, $F = 0.76$, $df = 3,19$, $P = 0.53$) but was significantly different between depths ($F = 413.41$,

$df = 1,19$, $P < 0.001$). The interaction term (site \times depth) was removed from the model after an initial analysis revealed it was not statistically significant ($P = 0.12$). During a sunny summer day near noon-time, mean PFD for all sites attenuated from $1,237 \pm 25 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at 2 m to $558 \pm 20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at 10 m.

Wave exposure

Analysis of clod card dissolution rates revealed a significant interaction between site and depth (depth \times site; $F = 18.98$; $df = 3,87$; $P < 0.001$) because flow attenuated less with depth at the wave-protected sites than at the wave-exposed sites. Therefore, differences in relative water motion between depths at wave-exposed and wave-protected sites were tested by measuring dissolution of gypsum blocks while differences in flow velocities between shallow exposed and protected sites were tested using maximum wave force dynamometers. The January 2000 flow estimations using gypsum blocks submerged for 10 days revealed significant attenuation of flow for both wave-exposed and wave-protected sites (wave-exposed $F = 148.47$, $df = 1,18$, $P < 0.001$; wave-protected $F = 139.45$, $df = 1,18$, $P < 0.001$). During the October 2000 dynamometer measurement period, maximum water velocities at the shallow wave-exposed sites were twice that of wave-protected sites. Mean maximum water velocity measured was $2.85 \pm 0.15 \text{ m s}^{-1}$ at the wave-exposed sites and $1.41 \pm 0.01 \text{ m s}^{-1}$ at the wave-protected sites (t test $t = 9.40$, $df = 4$, $P < 0.001$). The overall flow regime during the water velocity measurements was typical for that time of year and likely underestimated the maximum wave forces experienced annually. In the winter, storms can produce waves with presumably much higher velocities at the exposed sites than were recorded in October.

Relative abundance of *Pachydictyon coriaceum*

There was no significant effect of wave exposure on the number of *Pachydictyon coriaceum* thalli per square

Table 1 *Pachydictyon coriaceum* thallus density, percent cover, and blade proliferation means (\pm SE, $n = 30$) between wave-exposed and wave-protected sites at 2 and 10 m

	2 m		10 m	
	Exposed	Protected	Exposed	Protected
Proliferation index	3.0 ± 0.19	2.0 ± 0.10	2.0 ± 0.18	1.0 ± 0.08
# of thalli/m ²	4.7 ± 0.47	5.6 ± 0.47	3.3 ± 0.44	1.9 ± 0.26
% cover	5 ± 1	25 ± 2	3 ± 1	8 ± 1

meter (exposure $F = 2.89$, $df = 1,246$, $P = 0.092$, Table 1). However, percent cover of *P. coriaceum* was higher at wave-protected sites compared to wave-exposed sites (exposure $F = 56.25$, $df = 1,246$, $P < 0.001$, Table 1) although a significant interaction between depth and exposure suggested that differences in percent cover depended on a combination of light attenuation and wave exposure. While thalli densities were similar at all shallow sites, those from wave-protected sites covered roughly five times more of the substratum versus those from wave-exposed sites. Thalli were significantly more proliferated at the wave-exposed sites compared to wave-protected sites (Mann–Whitney $U = 2851.5$, $df = 1$, $P < 0.001$).

At 10 m, percent cover of *Pachydictyon coriaceum* was higher at wave-protected sites compared to wave-exposed sites. The proportion of thalli that were proliferated at wave-exposed sites was significantly higher compared to wave-protected sites. (Mann–Whitney $U = 2891.5$, $df = 1$, $P < 0.001$.)

Thallus morphology

Principal components analysis performed on the suite of morphometric measurements revealed three orthogonal axes that explained 32.8, 26.0, and 24.6% of the variance, respectively (Table 2). PC1 was characterized by high positive loadings for widest blade width, narrowest blade width, and distance between branching, variables that describe the area of a given blade on a thallus. PC2 was characterized by high positive loadings for blade thickness and blade proliferation and negative loadings for widest blade width and distance between branching, variable combinations associated with a bushier, compact thallus. PC3 was characterized by high positive loadings for thallus surface area and volume. Factor loadings from individual thalli at each site at 2 and 10 m were plotted on the first two orthogonal axes to visualize any separation

of morphs from the different light and flow environments (Fig. 4). Analysis revealed a separation by gross morphology defined by the first two components between shallow wave-exposed thalli (wave-exposed morph) versus shallow wave-protected thalli (wave-protected morph). Separation was not as obvious at 10 m, suggesting a common morphology for all deep thalli where both light and flow are attenuated (deep morph).

Results from MANOVA indicated a significant difference in component loadings among morphotypes (Wilks' Lambda = 0.52; $F = 9.81$, $df = 6,150$, $P < 0.0001$). Comparison of individual variables from thalli collected at 2 m revealed significant differences between wave-exposed and wave-protected sites (Blade thickness $F = 26.42$, $df = 2,77$, $P < 0.0001$; Widest blade width $F = 3.36$, $df = 2,77$, $P = 0.04$; Branch length $F = 5.97$, $df = 2,77$, $P < 0.01$; Blade proliferations $F = 24.16$, $df = 2,77$, $P < 0.0001$). Blades

Table 2 Principal components analysis of morphological variables measured on *Pachydictyon coriaceum*

Variable	Loading scores		
	PC1	PC2	PC3
Widest blade width (WW)	0.885	−0.027	0.264
Narrowest blade width (NW)	0.884	0.221	0.252
Length between branches (LBB)	0.762	−0.198	0.119
Blade thickness (BT)	0.114	0.858	0.100
Proliferation (BP)	−0.133	0.868	0.251
Surface area (SA)	0.110	0.431	0.850
Volume (VOL)	0.333	0.235	0.882
Variance explained (%)	32.84	26.08	24.61
Eigen value	3.11	1.97	0.71

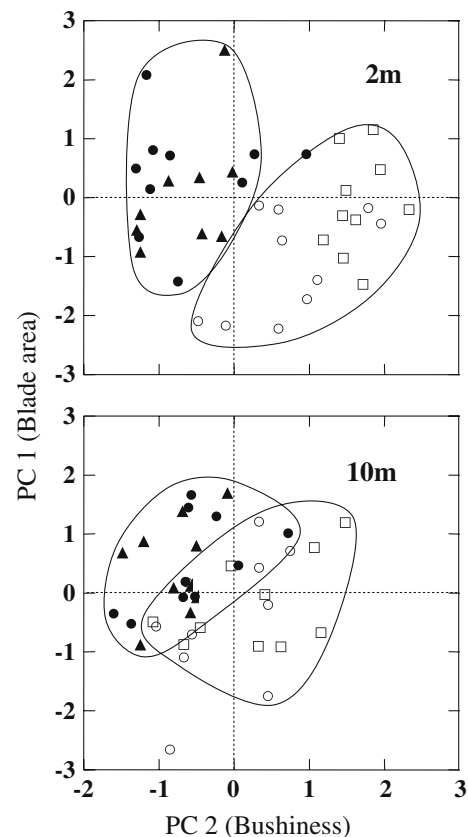


Fig. 4 Plot of Principal Component 1 (PC1, variables defining thallus bushiness) against Principal Component 2 (PC2, variables defining thallus blade area) for 2 and 10 m wave-exposed and wave-protected thalli. Thalli collected from wave-protected sites are represented by solid symbols: Blue Cavern (filled triangle), the Quarry (filled circle). Thalli collected from wave-exposed sites are represented by open symbols: Bird Rock (open square), Isthmus Reef (open circle)

Table 3 Morphological characteristics of *Pachydictyon coriaceum* thalli collected from three environments (mean (SE, $n = 10$))

	Wave-exposed 2 m	Wave-protected 2 m	All sites 10 m
Blade thickness (mm)	0.33 ± 0.02	0.20 ± 0.01	0.22 ± 0.01
Widest blade width (mm)	9.30 ± 0.42	12.07 ± 0.47	11.06 ± 0.38
Branch length (cm)	7.39 ± 0.31	9.84 ± 0.39	9.73 ± 0.44
Blade proliferations (%)	81 ± 0.05	15 ± 0.08	0.30 ± 0.06

from thalli collected at wave-exposed sites were thicker, narrower, shorter between branches, and more proliferated than those collected at wave-protected sites (Table 3).

Surface area:volume ratios

Analysis of covariance of thallus surface area and thallus volume revealed significantly different slopes for thalli from three environment types: 2 m wave-exposed, 2 m wave-protected and 10 m (volume \times environment $F = 9.84$, $df = 2,74$, $P < 0.001$; Fig. 5). Preliminary ANCOVA analyses provided the rationale for pooling sites as slopes for SA:V were homogeneous for all deep sites, for wave-exposed sites, and for wave-protected sites. Among thalli from each environment, surface area increased fastest per unit volume for the wave-exposed morph, followed by the deep morph, then the wave-protected morph.

NP versus PFD

The parameters P_{\max} , I_k , and α were estimated for the three morphotypes from NP versus PFD curves

(Table 4). Among the three morphs, the shallow wave-exposed thalli had the lowest NP_{\max} and α , suggesting reduced photosynthetic efficiency at both low and high PFD. At flow velocities of 9.5 cm s^{-1} , all morphotypes were light saturated above $190 \mu\text{mol photons s}^{-1} \text{ m}^{-2}$.

Morphology and NP

Maximum NP varied among morphotypes (ANOVA, $F = 20.55$, $df = 2,63$, $P = 0.008$, Table 5). The wave-protected and deep morphs had significantly higher rates of photosynthesis than the wave-exposed morph (Tukey post hoc comparison: wave-protected vs. deep, $P = 0.018$; wave-protected vs. wave-exposed, $P = 0.008$) suggesting that the thinner-bladed, broader morphotype is capable of higher rates of photosynthesis than the thicker-bladed, compact morphotype. There was no significant effect of the simulated environment treatment ($F = 1.50$, $df = 2,62$, $P = 0.232$), nor was the interaction of morphotype and treatment significant ($F = 1.52$, $df = 4,62$, $P = 0.207$) suggesting that the relationship between photosynthesis and morphotype is consistent across varying light and water flow environments.

Fig. 5 Plot of (thallus volume) $^{-3/5}$ against (thallus surface area) $^{-1/5}$ for the three morphotypes: wave-exposed (open square), wave-protected (filled circle), and deep (open triangle)

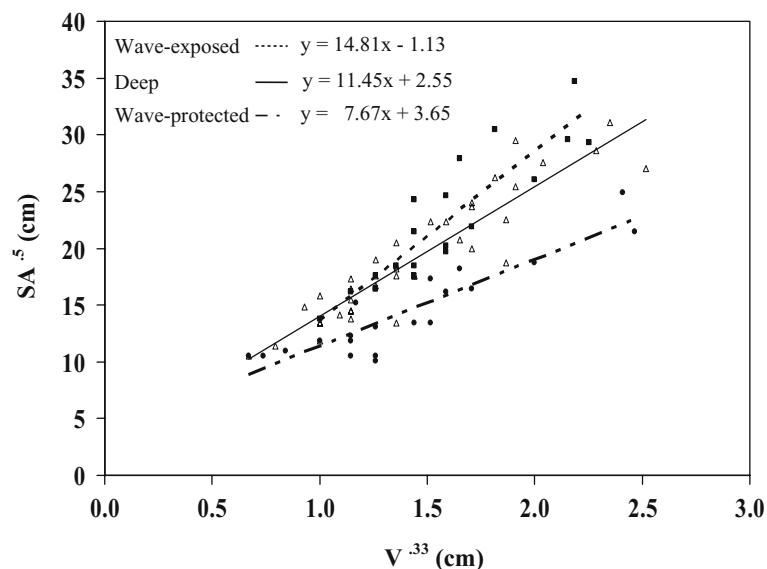


Table 4 Photosynthetic parameters (mean \pm SE, $n = 3$) of the three morphotypes

	P_{\max} (mmol O ₂ h ⁻¹ g dry mass ⁻¹)	I_k (μ mol photons m ⁻² s ⁻¹)	α (mmol O ₂ h ⁻¹ g dry mass ⁻¹ /μmol photons m ⁻² s ⁻¹)
Wave-exposed	0.26 \pm 0.04	200 \pm 60	0.0013 \pm 0.0005
Wave-protected	0.36 \pm 0.09	240 \pm 76	0.0015 \pm 0.0011
Deep	0.38 \pm 0.02	198 \pm 26	0.0017 \pm 0.0003

Table 5 Mean (\pm SE) biomass-specific NP (mmol O₂ h⁻¹ g dry mass⁻¹) for the three morphotypes in each simulated light/flow environment. $n = 8$ for each morphotype in each environment

	High flow/high light	Low flow/high light	Low flow/low light
Wave-exposed	0.31 \pm 0.03	0.28 \pm 0.03	0.24 \pm 0.05
Wave-protected	0.69 \pm 0.07	0.46 \pm 0.04	0.58 \pm 0.12
Deep	0.62 \pm 0.07	0.60 \pm 0.13	0.71 \pm 0.09

Morphology and drag

Drag coefficients of each morphotype decreased and converged with increasing water velocity and biomass-specific drag increased with water velocity. The wave-exposed morph had a lower C_d than the other morphs at 7.5 and 16 cm s⁻¹ (Table 6). Values of E for each morphotype were negative, suggesting thallus reconfiguration and compaction and a reduction in C_d as velocity increased (Table 6). Although the wave-exposed morph had the lowest C_d of the three morphs at a given flow speed, the wave-protected morph exhibited significantly greater compaction with increased

velocity (ANOVA, $F = 17.31$, $df = 2,27$, $P < 0.0001$; Tukey post hoc comparison: wave-protected vs. wave-exposed, $P < 0.0001$; deep vs. wave-exposed, $P = 0.32$; wave-protected vs. deep, $P < 0.001$). The E value for the wave-protected morph was 27% greater than the deep morph and 40% greater than the wave-exposed morph.

Mean thallus length of the wave-exposed morph was 10.7 \pm 1.2 cm, the mean thallus length of the wave-protected morph was 16.7 \pm 2.9 cm, and the mean thallus length of the deep morph was 13.1 \pm 2.5 cm. Thallus lengths between morphs were significantly different (ANOVA on log transformed data, Tukey post hoc test: wave-protected vs. wave-exposed, $P < 0.001$; deep vs. wave-exposed, $P = 0.03$; wave-protected vs. deep, $P = 0.008$).

Discussion

The results of this study demonstrate that the morphology of *Pachydictyon coriaceum* varies depending on the physical environment in which it grows and that wave exposure is a major factor shaping morphology with depth (i.e., light attenuation) becoming important in habitats where water flow is reduced.

The morphology of thalli from the wave-exposed sites can be characterized as highly-branched and compact (see Fig. 1a). This morphology can have hydrodynamic advantages over a flabellate morphology. Flexible, branched shapes can reconfigure in flow and become more streamlined, reducing drag (Vogel 1984; Carrington 1990; Gaylord et al. 1994). Further, a highly-branched morphology can dampen turbulent flow passing through the thallus (Anderson and Charters 1982) thereby reducing drag. Gaylord (2000) has observed that flatter algae tend to experience higher accelerational forces and suggested that thallus fluttering could be a possible mechanism for those forces.

Although not addressed experimentally, mensurative data suggest that the thallus morphology from wave-exposed sites is influenced by damage (tattering) and subsequent proliferative regrowth. At shallow wave-exposed sites the mean proportion of blade tip proliferation was over 70% and less than 30% at

Table 6 Drag coefficients and, E , “Vogel’s number” for the three morphotypes at different flow velocities, u (means \pm SE, $n = 10$)

u	C_d (\pm SE)	E (\pm SE)
Wave-exposed		
0.08	0.26 \pm 0.03	–
0.16	0.11 \pm 0.01	–
0.31	0.06 \pm 0.01	–
0.39	0.04 \pm 0.01	–
0.47	0.03 \pm 0.01	–1.13 \pm 0.05
Wave-protected		
0.08	0.55 \pm 0.08	–
0.16	0.21 \pm 0.02	–
0.31	0.07 \pm 0.01	–
0.39	0.05 \pm 0.01	–
0.47	0.04 \pm 0.01	–1.59 \pm 0.08
Deep		
0.08	0.38 \pm 0.04	–
0.16	0.17 \pm 0.02	–
0.31	0.07 \pm 0.01	–
0.39	0.05 \pm 0.01	–
0.47	0.04 \pm 0.01	–1.25 \pm 0.04

shallow wave-protected sites. Blanchette (1997) found incidences of tattering in *Fucus gardneri* transplanted from wave-protected to exposed intertidal sites and suggested that tattering may increase survival in wave-exposed environments by reducing thallus size. Several seaweeds have been shown to produce adventitious branches following mechanical damage to the blades, especially the apices. Perrone and Felicini (1972) found proliferations could be induced in *Pteroglossum nicaeense* (Rhodophyta) by cutting the blades at the tips and found similar results with *Gigartina acicularis*. Van Alstyne (1989) induced adventitious branches by clipping *Fucus distichus* in the field. Further, Gaillard et al. (1986) found that when *Dictyota dichotoma* is damaged, adventitious fronds always are generated by the cortical cells and that apical cells control the position, number, and size of proliferations. Similar growth activity appears to occur with *P. coriaceum*, as its blades terminate with a single, large apical cell (Abbott and Hollenberg 1976).

An alternative hypothesis that herbivory from mesograzers is the cause of damage resulting in proliferations was not addressed experimentally and cannot be ruled out. However, preliminary data indicated no differential abundance of mesograzers among proliferated and non-proliferated morphotypes. Although bite marks were observed, they were rare and could be found on all morphotypes. Most importantly, observations of wave-exposed thalli revealed that most damage resulting in blade proliferations were straight, resembling tears, not bite marks. The hypothesis that bite marks from mesograzers could facilitate blade tattering by creating weak points has been addressed in the literature (Black 1976; Koehl and Wainwright 1977; Padilla 1993) and warrants further examination.

The thalli collected at deep sites were foliose and monolayered. Clod card data indicate that water motion for these habitats is reduced relative to shallow sites. In the absence of damaging water flow, other physical factors associated with depth (e.g., light attenuation) may influence the morphology of *Pachydictyon coriaceum*. Thalli from all sites at 10 m were skewed toward the positive loadings of PC1, which was defined by blade area. The thalli from deeper habitats tended to have wider and longer blades that can capture more light. Also, blades of the deep morph were thinner compared to blades from shallow thalli. Thin blades can allow light to pass through them, mitigating the effects of self-shading for the entire thallus (Hay 1986). Thin blades have been shown to photosynthesize more efficiently than thick blades for several macroalgal species (King and Schramm 1976; Lüning

and Dring 1985; Gerard 1988; Peckol and Ramus 1988; Enriquez et al. 1995).

Mean SA:V ratios of thalli from shallow wave-exposed sites were significantly higher than those from shallow wave-protected sites. This may be due to tattering of blades and subsequent proliferative regrowth. High water velocities may alter overall surface area of the thallus by tattering larger blades that later re-grow into multiple smaller blades densely packing the added surface area into a highly-branched form.

A significant difference in SA:V ratios was found between depths within the wave-protected sites. Thalli from deep environments were broader, thinner and flatter. This suggests that SA:V ratios of *P. coriaceum* increase with depth and may facilitate capturing light more efficiently. Thalli with a larger planar surface can persist at wave-protected sites because they are not exposed to the damaging effects of high water motion. It is likely that in wave-exposed environments, water flow at damaging velocities (i.e., strong enough to cause tattering) shapes SA:V ratios in *Pachydictyon coriaceum*, while depth affects SA:V of thalli in the absence of damaging flow velocities.

Results from the field censuses suggest that there may be an optimal environment in which *Pachydictyon coriaceum* thrives (sensu Cheshire and Hallam 1989; Jakelman and Bolton 1990), one of moderate water motion and high light. The wave-protected morph had a low incidence of blade proliferation, was more abundant than thalli growing at 10 m, and covered about five times more of the substratum than wave-exposed thalli or deep thalli. Further, thalli from the wave-protected sites were greater in size and biomass than thalli from the other environments. These patterns suggest that in these environments *P. coriaceum* may be more competitive, faster growing, and/or have a higher survivorship. However, morphological plasticity increases the ecological success of *P. coriaceum* by facilitating survival in physical habitats outside its optimal environment.

This study indicates that a tradeoff exists between photosynthetic efficiency and drag reduction for the morphotypes only at lower water velocities (8–21 cm s⁻¹), as the differences in drag are negligible at higher flow velocities. The thicker bladed wave-exposed morphs had the lowest C_d among the three morphotypes across all flow velocities while also exhibiting the lowest biomass-specific NP for the three simulated light/flow environments. The wave-protected and deep morphs outperformed the wave-exposed morph in terms of photosynthesis but experienced higher drag per biomass.

The E values for the three morphs were negative as theory predicts for flexible objects that streamline. The E values for *Pachydictyon coriaceum* were more negative than those of other macroalgae tested (Gaylord et al. 1994) and may be the result of two factors. First, *P. coriaceum* is a delicate, subtidal alga and is more flexible than larger kelps (Order Laminariales) or tougher intertidal species. Second, drag was measured over a smaller velocity range (0.08–0.47 m s⁻¹) and the greatest amount of change in shape for flexible objects occurs at lower flow velocities. The wave-protected morph experienced the greatest degree of reconfiguration from its still-water shape as flow velocities increased. The highly-branched wave-exposed morph experienced the least degree of reconfiguration from its still-water shape. Furthermore, mean C_d for the wave-exposed morph at low flow velocities ($u = 0.08$ m s⁻¹) was half that for the wave-protected morph suggesting the wave-exposed morph is more streamlined than the other morphs.

The compact shape of the wave-exposed morph requires less reconfiguration to reduce drag than the other morphotypes. However, the densely-bladed thallus shades many of its internal blades. This self-shading could account for the lower biomass-specific NP of the wave-exposed morph. Self-shading has been shown to reduce photosynthetic performance in turf algae (Williams and Carpenter 1990) and temperate macroalgae, including other Dictyotales (Stewart and Carpenter 2003). Blades of the wave-exposed morph were ~1.5 times thicker than the wave-protected morphs, which may mitigate damage at higher flow velocities. However, thicker blades can have negative effects on thallus photosynthetic performance (Enriquez et al. 1995). A difference in photosynthetic pigment composition among morphs was not addressed in this study and is an alternative to the hypothesis that gross thallus morphology reduces NP under certain flow conditions. However, observations of thallus compaction of wave-exposed morphs in both flume experiments suggest self-shading is the most parsimonious explanation for lowered NP.

At water velocities >31 cm s⁻¹, the tradeoff between NP and drag is obscured as drag coefficients of the three morphotypes converged with increasing flow velocities. Carrington (1990) demonstrated similar results of converging C_d for several intertidal algae species with varying morphologies and proposed that drag forces are not influenced strongly by algal morphology. The results of this study suggest that morphology accounts for differences in drag forces on *Pachydictyon coriaceum* at lower flow velocities. At higher flow velocities, selected components of thallus morphology

(e.g., differential size, holdfast attachment strength, stipe and/or blade thickness) likely are more important than overall morphology in determining the longevity of a thallus in a high flow environment. The smaller size and thicker blades of the wave-exposed morph, not its streamlined shape, probably allows it to persist in high water velocity environments whereas the other morphs are absent.

It is unclear if morphology is important in mitigating potential accelerational forces on the thallus of *Pachydictyon coriaceum*. Gaylord et al. (1994) proposed that the intricate structure of seaweeds traps seawater within their interstices making a contribution to the added mass component that could increase the accelerational force experienced. Therefore, a morphology that minimizes interstitial volume should encounter lower accelerational forces (all else being equal). Because the compact wave-exposed morph has less interstitial volume, its added mass is less and it probably would experience lower accelerational forces compared to the wave-protected morph. However, this hypothesis warrants in situ experimentation, as measurements in the intertidal by Gaylord (2000) demonstrated that fluid accelerations there occur on spatial scales too small to impose large loads on the thallus.

The results of this study suggest that environmentally-driven changes in thallus morphology can influence both photosynthesis and, to a lesser degree, hydrodynamic forces acting on *Pachydictyon coriaceum*.

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