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Visualization of seawater flow around morphologically distinct forms of the giant kelp *Macrocystis integrifolia* from wave-sheltered and exposed sites

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Abstract

Our objective was to determine whether blades of *Macrocystis integrifolia* from a wave-sheltered site possess morphological features that "trip" velocity boundary layers (VBL) from laminar to turbulent in conditions of low water motion, compared to blades from a wave-exposed site. The movement of seawater around morphologically distinct blades of *M. integrifolia* from wave-sheltered and exposed sites was visualized in a recirculating flow tank in which seawater flow was initially laminar at velocities up to 8 cm s^{-1}. Turbulent VBLs were observed for both blade morphologies at free-stream seawater velocities of 2 cm s^{-1}, and at a Reynolds numbers of between 10^2 and 10^4, which is lower than that predicted from boundary layer theory. Flow around blades from a wave-sheltered site was dominated by separation induced by large edge undulations. For the wave-exposed morphology, the flow pattern was similar to that along a smooth, flat plate, but the observed thickness of the VBL was up to a factor of 2 greater than that predicted from laminar or turbulent boundary layer theory. There were no obvious differences in how structural features such as marginal spines and bulbs affected seawater flow around the different blade morphologies.

Nearshore coastal regions play host to a dramatic range of water velocities. Protected embayments may be subject only to tidal changes in water level and velocities that rarely exceed 10 cm s^{-1}, whereas shoreline exposed to the full impact of the open ocean might experience waves that generate transient velocities of up to 14 m s^{-1} (Hiscock 1983; Bell and Denny 1994). Seaweeds growing in nearshore environments are subject to a range of stresses associated with the degree of water motion they encounter, where stress is a collective term for the external factors that limit dry matter production (Dring 1982). At wave-exposed sites, drag forces that damage or remove blades and entire plants are considered the main hydrodynamic factor reducing productivity (Wheeler 1988), whereas in areas that experience seawater velocities <4–6 cm s^{-1}, seaweed productivity may be limited by the development of a thick diffusion boundary layer that reduces the transport of essential inorganic nutrients to the blade surface (Wheeler 1980; Hurd et al. 1996).

It is well known that blade morphologies of the Laminariales (kelps) vary with the degree of water motion in which they grow (e.g. Norton 1969; Druehl and Kemp 1982; Norton et al. 1982; Koehl and Alberte 1988), so that when adult sporophytes are transplanted from one habitat to another, the new blade growth is similar to that of plants native to that environment (e.g. Norton 1969; Druehl and Kemp 1982; Gerard and Mann 1979). This plastic response to water motion has prompted the suggestion that, by changing their morphology, kelps are able to modify their hydrodynamic environment and thereby alleviate or reduce drag or diffusion stress at wave-exposed and sheltered sites, respectively (Neushul 1972; Wheeler 1988; Norton et al. 1982).

Fluid flow is characterized as being laminar, turbulent, or in a transitional state between the two regimes (*see* Wheeler 1988, Figure 3). Under ideal experimental conditions, when seawater flows in an initially laminar fashion over a smooth flat plate, viscosity creates a laminar velocity boundary layer

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This paper is dedicated to John Boom, who is sadly missed.

(VBL) where velocity varies from zero at the flat-plate surface (i.e. the no-slip condition) to that of the free-stream flow. At some distance downstream of the leading edge, viscous forces are no longer able to dampen out disturbances in the flow and the VBL makes the transition to turbulence. Growth of the turbulent region means that the total thickness of the VBL increases as the observer moves downstream, but the thickness of the viscously dominated region, termed the viscous sublayer (VSL), decreases (Schlichting 1979; Wheeler 1988).

Ions move across a laminar VBL or VSL by molecular diffusion (Denny 1988). If the surface in contact with seawater is a seaweed thallus actively taking up ions from the surrounding seawater, then a concentration gradient forms, termed the diffusion boundary layer (DBL). As for the VBL, the thickness of the DBL decreases with increasing seawater velocity (Wheeler 1988; Koch 1994; Hurd et al. 1996). Under steady-state conditions, the maximal thickness of the DBL can equal that of the laminar VBL or VSL (C. L. Stevens and C. L. Hurd in prep.). Therefore, if the VBL surrounding a seaweed is laminar, the potential thickness of the DBL is greater than when the VBL is turbulent.

The dimensionless Reynolds number (Re) is a useful estimate of whether fluid flow around an object is dominated by viscous or turbulent (inertial) forces (Vogel 1994). When laminar flow encounters the leading edge of a smooth, flat plate, the transition to turbulence occurs at a distance downstream characterized by Re of 5×10^5–10^6; flow is viscously dominated prior to this point (Schlichting 1979). For a 0.5-m-long kelp blade experiencing free-stream seawater velocities of $\sim$0.06 m s^{-1}, Re = 2×10^4. This observation led Wheeler (1988) to suggest that at low velocities, seawater flow around kelp blades is viscously dominated and laminar VBLs are predicted. If this were the case, the potential thickness to which the DBL could grow is greater than if the VBL were turbulent, and the rate of transport of essential nutrients to the blade surface would be reduced.

If the thickness of diffusion boundary layers limits mass transport, then "aquatic plants should have evolved morphologies that would 'trip' laminar boundary layers to turbulent boundary layers with thinner sub-layers" (Wheeler 1988, p. 32). Mass transport of nutrients is reduced at free-stream seawater velocities of <4–6 cm s^{-1} (Wheeler 1980; Hurd et al. 1996). Therefore, a blade morphology that promotes the transition to turbulence would be advantageous for kelp growing in environments where such low velocities are common.

Our objective was to determine whether blades of kelp growing in a wave-sheltered environment possess morphological features that allow increased inorganic nutrient acquisition compared to blades of the same species from a wave-exposed site. We chose the giant kelp *Macrocystis integrifolia* as the test species because it possesses a morphology that varies with the degree of exposure to water motion. Blades of plants from wave-sheltered sites are wide, thin in cross-section, with large edge undulations and marginal spines that arise at irregular angles from the blade. In contrast, blades from exposed sites are narrow, thick in cross-section, flat, and have a densely corrugated surface and marginal spines flush to the blade (Pace 1972; Druehl and Kemp 1982; Hurd et al. 1996). In the laboratory visualization experiments reported here, seawater flow around blades of *M. integrifolia* from wave-sheltered and exposed sites was compared in order to determine the structure of the VBL around both blade morphologies at a range of seawater velocities, elucidate the relative importance of different blade morphological features that affect the VBL structure, and evaluate whether the sheltered blade morphology can result in enhanced nutrient transport across the diffusion boundary layer at low seawater velocities compared to the exposed blade.

Materials and methods

Experimental design—At the onset of this study, the morphological features of *M. integrifolia* that most affected fluid flow were not known. To avoid a priori assumptions as to which of these features might be most important, we used whole, live blades of *M. integrifolia* in the visualization experiments. Visualization experiments were designed to complement a set of laboratory experiments in which the rate of inorganic nitrogen uptake and the thickness of the diffusion boundary layer were estimated for wave-sheltered and exposed blades of *M. integrifolia* from the same sites (Hurd et al. 1996). The sample size of blades used in visualization experiments was small ($n = 2$ for each site) owing to time constraints in data processing; however, the morphological parameters of these *M. integrifolia* blades were within the ranges of those recorded for blades in the nitrogen uptake experiments ($n = 16$; Hurd et al. 1996).

Collection of M. integrifolia *and morphological measurements*—Individual blades of *M. integrifolia* Bory were collected from two sites at Dixon Island, Barkley Sound, British Columbia (48°51.24′N, 125°7′W), in February and June 1993 (four blades total). One site was sheltered from, and the other exposed to, wave action; blades from each site possessed the morphology predicted for that site (Hurd et al. 1996). Blades were wrapped in seawater-soaked newspaper and transported on ice to the University of British Columbia at Vancouver where they were stored in cold seawater for up to 7 d. The following morphological parameters were measured to the nearest centimeter: bulb width, blade length, maximum blade width, and maximum blade edge undulation peak-to-peak height (Fig. 1). Base angle and the number of surface corrugations per centimeter blade width were estimated from photographs of the blade. The frontal area was defined as surface area perpendicular to the direction of the flow. Bulb frontal area (A) was estimated from the maximum bulb width (w) as $A = \pi w^2/4$. Total blade frontal area was the product of the maximum blade width and the blade edge undulation peak-to-peak height.

Flow visualization—Visualization experiments were conducted in a 46-liter recirculating flow tank in which seawater flow was laminar at free-stream velocities of up to 8 cm s^{-1} (Fig. 2; Hurd et al. 1994). A single blade of *M. integrifolia* was attached to a false floor in the test section with a fine pin inserted through the bulb. Time-lapse photography of two tracers was used to visualize the flow. A slurry of the

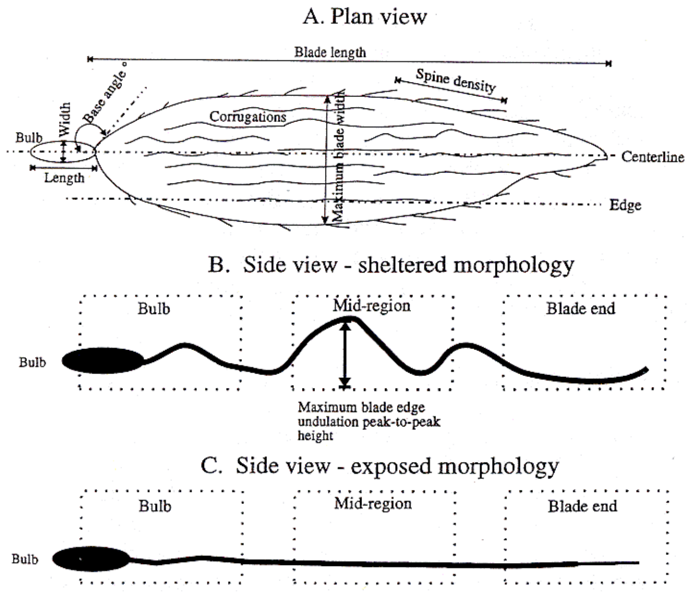

Fig. 1. Schematic showing morphological parameters measured for blades of *Macrocystis integrifolia* collected from a wave-sheltered site and an exposed site in February and June 1993. A. Plan view showing the longitudinal blade centerline and edge positions used in visualization experiments. B, C. Side views illustrate the edge undulations of the sheltered blade (B) compared to the relatively flat profile of the exposed morphology (C). Square boxes indicate the bulb, middle, and end of blade regions visualized in experiments.

reflective resin Pliolite (25 ml, 100–295-μm diameter) was added to the tank and used to create particle streaks. Additionally, the fluorescent dye sodium fluorescein was injected through a thin tube into the flow upstream of the kelp blade by using a gravity feed system, thereby permitting qualitative estimation of the residence time of fluid within regions of the boundary layer.

In the first set of experiments (February 1993), a projector suspended over the tank provided the required light source (Hurd et al. 1994), while a 5-W Argon-Ion laser and a scanning mirror replaced the projector in the second set of experiments (June 1993; Fig. 2). The enhanced intensity of the laser greatly improved the resolution and signal-to-noise ratio of images obtained, allowing superior quantitative analysis. Images were recorded with a 35-mm SLR camera and a COHU 4910 CCD camera with a Sony Hi-8 video recorder. Long focal-length lenses were used to reduce image distortion.

For each particle tracking experiment, a single *M. integrifolia* blade was placed in the flow tank and the tracer was added. The cameras were focused on specific locations along the blade, and images of the selected location were recorded at seawater velocities ranging from 0.5 to 8 cm s^{-1}. The cameras were then moved to the next position and the process repeated. Positions selected included the region immediately behind the bulb, the midregion of the blade, and the blade end (Fig. 1B,C) for two longitudinal sections of the blade, i.e. the blade centerline and the blade edge (Fig. 1A).

Images recorded on video were digitized with a Perceptics (Pixel Buffer/Pixel Store) 8-bit frame grabber housed in a Mac IIfx. Six consecutive frames were digitized from video, and an image-processing routine analyzed pairs from this group using spatial cross-correlations to infer a quantitative

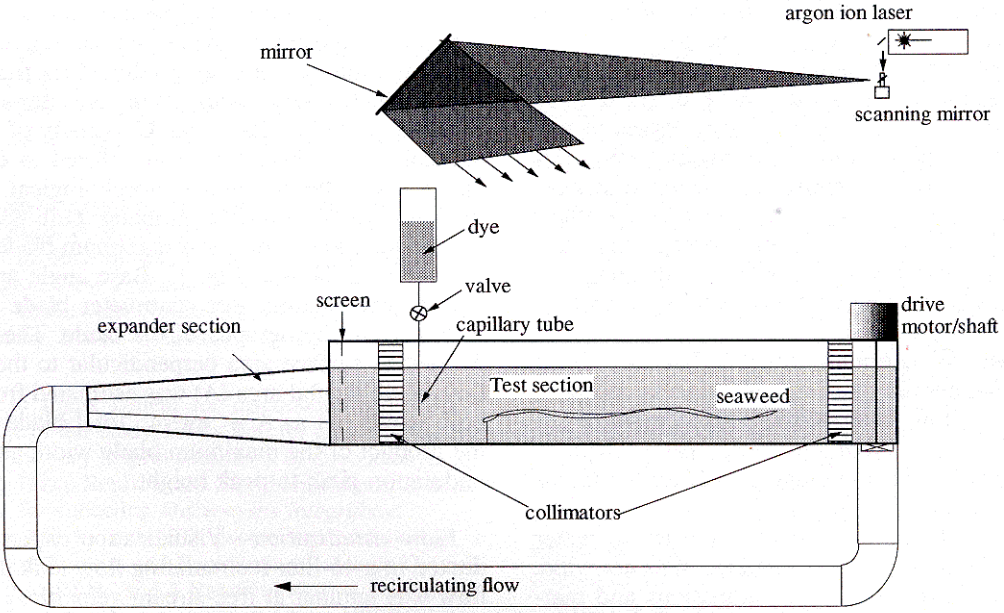

Fig. 2. Schematic of the unidirectional laminar-flow tank used in visualization experiments. An intense light sheet was provided with an Argon-Ion laser and dye was injected through a thin tube. Working section is 15 cm high × 20 cm wide. Total volume = 46 liters.

Table 1. Morphological parameters for each *Macrocystis integrifolia* blade used in visualization experiments in February and June 1993. ND—no data.

Blade parameters	Sheltered		Exposed	
	Feb	Jun	Feb	Jun
Max blade width (cm)	11.5	10	7.0	8.7
Max undulation amplitude (cm)	3.1	3.2	1.4	0
Blade length (cm)	49.5	44	52.5	54
Bulb width (cm)	1.2	1.1	1.5	1.5
Bulb length (cm)	4.2	4.1	4.9	5.6
Base angle (°)	131	ND	152	ND
Spine density (spines cm^{-1})	1.5	4.5	1.4	4.7
Corrugation density (corrugations cm^{-1})	1	2	2.4	2
Bulb frontal area (cm^2)	1.13	0.95	1.77	1.77
Total blade frontal area (cm^2)	36	32	10	2.1
Bulb frontal area as % of total blade frontal area	3	3	18	84

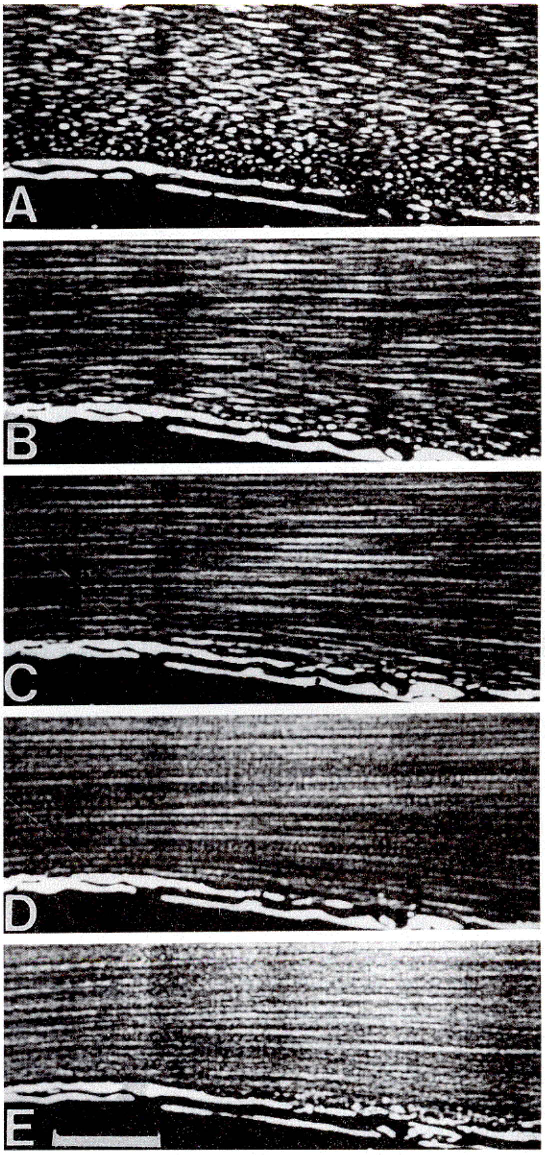

Fig. 3. Streaklines along the centerline of the mid-region of *Macrocystis integrifolia* from a wave-exposed site in February 1993, at a range of free-stream seawater velocities—(A) 0.5 cm s^{-1}, (B) 1 cm s^{-1}, (C) 2 cm s^{-1}, (D) 4 cm s^{-1}, (E) 8 cm s^{-1}. Seawater is moving left to right in all photographs, scale bar (E) = 1 cm.

two-dimensional velocity field (Stevens and Coates 1994). Image sequences also were added so that the particle images formed streaklines and a qualitative picture of the flow field was thus derived.

Results

Blade morphology—M. integrifolia blades from the wave-sheltered site were wider, shorter, and had smaller bulbs than did blades from the exposed site (Table 1). The exposed blade in February had more corrugations per centimeter of blade width than did the sheltered blade, whereas in June the corrugation density was similar for sheltered and exposed blades. Spine density was similar for sheltered and exposed blades, although blades in June had more spines per centimeter than did blades in February. The sheltered blade used in February had five undulations and the June blade three undulations along each edge.

Flow visualization—Visualization data were obtained from three regions along the centerline of the exposed blades: immediately behind the bulb, the blade midregion (12.5 cm in February; 15 cm in June), and the blade end (38 cm in February; 37 cm in June). Data also were obtained along the blade edge of the midregion.

The largest Re in any experiment was 5×10^4, a factor of 10 less than the critical Re for transition to turbulence for a boundary layer (i.e. $<5\times10^5$); Re ranged down to 10^2. For all regions tested, turbulence was observed at Re substantially lower than the critical value. At free-stream seawater velocities <2 cm s^{-1}, a laminar VBL was observed in the blade midregion, whereas the boundary layer was turbulent at free-stream velocities of ≥ 2 cm s^{-1}. At the blade end, the VBL was turbulent at free-stream velocities of 0.5 cm s^{-1}.

Seawater flow along the centerline of the exposed blade morphology was similar in general form to that over a flat plate (Figs. 3, 4); the gradient region of the velocity profile becomes thinner with increasing free-stream seawater velocity (Fig. 4). Quantitatively, it is possible to compare observations with values predicted from flat-plate boundary layer theory. The thicknesses of observed VBLs were about a factor of 2 greater than those predicted by laminar (*in* Vogel 1994, equation 8.1) or turbulent (*in* Vogel 1994, equation 8.8) boundary layer theory. Strictly, however, it is inappropriate to apply these equations to the systems under consideration. Because turbulence was observed at a Re below values critical for the transition to turbulence adjacent to a flat plate, neither equations for laminar (because turbulence was observed) nor turbulent boundary layer (because Re $<5\times10^5$) conditions should be applied. The velocity profiles

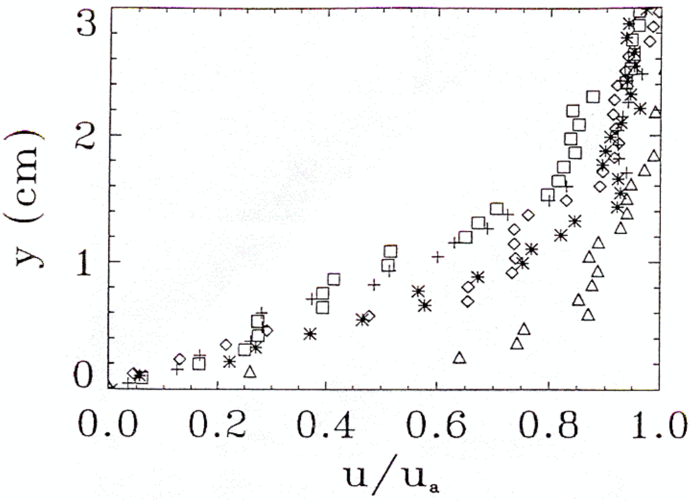

Fig. 4. Vertical velocity profiles of seawater flow along an the centerline of an exposed blade of *Macrocystis integrifolia* at a range of free-stream velocities (u_a): 0.5 cm s^{-1} (□), 1 cm s^{-1} (+), 2 cm s^{-1} (∗), 4 cm s^{-1} (◇) and 8 cm s^{-1} (△). y is the vertical distance above the blade surface and u is the actual horizontal velocity (determined by using image analysis techniques), which is normalized to u_a.

taken from the edge of the midblade region were similar to those of the centerline, suggesting that there was no obvious systematic three-dimensional circulation around the blade.

The general enhancement of the level of turbulent energy along the exposed blade is due to the combined effects of the frontal area, bulb, spines, and surface corrugations. Of these features, the effect of the bulb was the most obvious in our experiments and presumably serves to quicken the transition to turbulence. However, the small width of the bulb compared to the total blade width means that this feature plays a secondary role in overall boundary layer development along the blade. At free-stream velocities of 0.5 and 1 cm s^{-1}, dye streaks revealed a laminar recirculating eddy behind the bulb. At 2 cm s^{-1}, laminar separation occurred; at ≥4 cm s^{-1}, the eddies formed behind the bulb were shed downstream, generating a vortex street. At this free-stream velocity, flow behind the bulb was turbulent.

The leading edge spines were in view when flow along the blade edge was visualized, but had no apparent effect on seawater flow. Exposed blades were not observed to flap at any velocity tested (0.5–10 cm s^{-1}).

In February 1993, visualization data were obtained 12.5 cm downstream of the bulb for the centerline and edge for the sheltered blade. In June, data were obtained from three regions along the centerline: immediately behind the bulb, the blade midregion (23 cm), and the blade end (34 cm). Data were also collected for two regions along the blade edge: the midregion (23 cm) and the blade end (34 cm).

As for the exposed blade, turbulent VBLs around the sheltered blade morphology were observed at Re below those predicted using boundary layer theory. For the sheltered morphology, however, VBL structure was dominated by flow separation caused by the edge undulations. Separation was observed at all free-stream velocities tested (Figs. 5, 6).

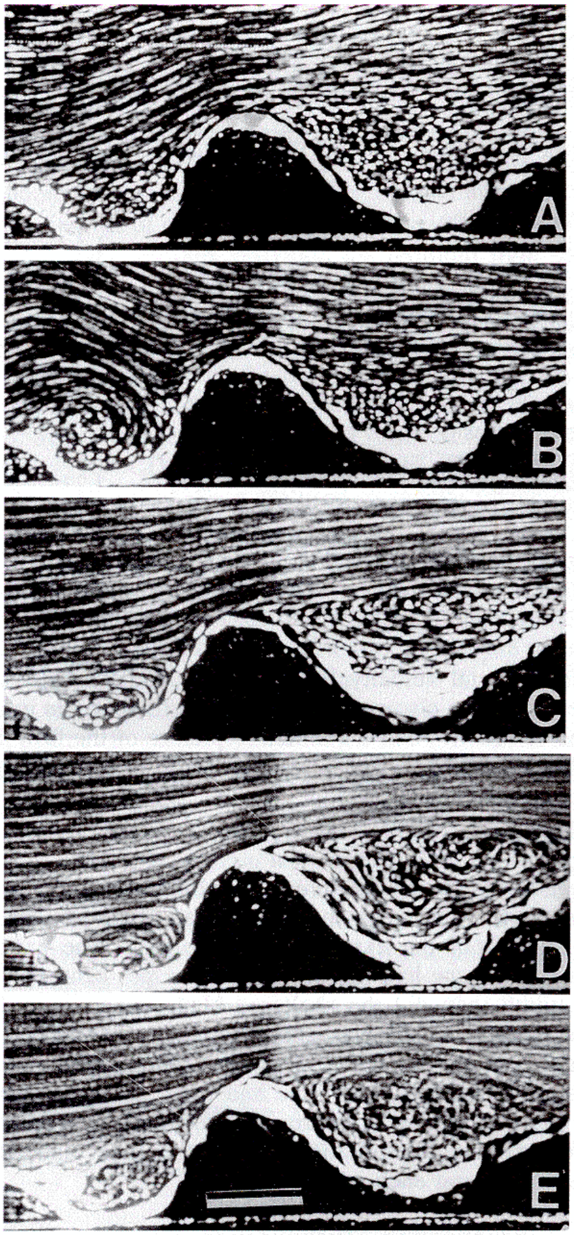

Fig. 5. Streaklines around two edge undulations blades of *Macrocystis integrifolia* from a wave-sheltered site in February 1993, at a range of free-stream seawater velocities—(A) 0.5 cm s^{-1}, (B) 1 cm s^{-1}, (C) 2 cm s^{-1}, (D) 4 cm s^{-1}, and (E) 8 cm s^{-1}. Seawater is moving left to right in all photographs, scale bar (E) = 1 cm.

Streaklines around a pair of undulations along the edge of the sheltered blade used in February show the formation of recirculating eddies that are the same approximate volume as the undulation (Fig. 5). For the larger undulation on the right-hand side, laminar separation is apparent at free-stream velocities of 0.5 and 1 cm s^{-1}, with laminar recirculation within the eddy (Fig. 5A,B). At 2 cm s^{-1}, it could not be determined whether flow within the large eddy was turbulent because the flow was dominated by motion associated with separation (Fig. 5C). At 4 cm s^{-1}, shear instabilities at the downstream end of the larger eddy led to exchange between

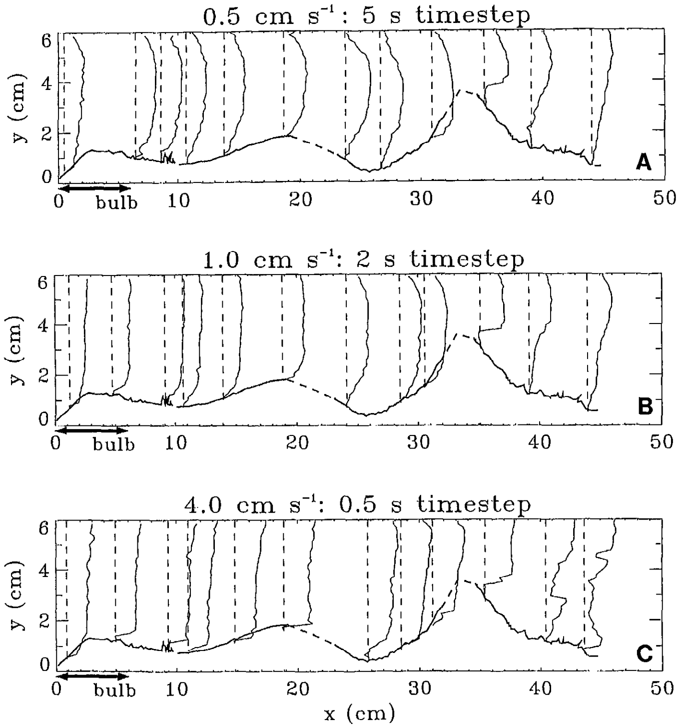

Fig. 6. Compilation of vertical velocity profiles along an undulate centerline of a *Macrocystis integrifolia* blade collected from a sheltered site in June 1993. The development of the VBL is shown at three free-stream seawater velocities—(A) 0.5 cm s^{-1}, (B) 1 cm s^{-1}, and (C) 4 cm s^{-1}. The horizontal solid line outlines the bulb and blade. y is the vertical distance above the blade surface and x is the distance downstream of the bulb. The figures illustrate how the flow field would move dye streaks injected normal to the flow (indicated by the dashed vertical lines along the blade) in a given timestep. The resulting velocity profile (solid vertical lines) depends on the blade morphology at each given starting point. Seawater is moving left to right. The vertical scale has been exaggerated.

the recirculating volume and the free-stream seawater flow, and flow within the eddy is turbulent (Fig. 5D). Shear instability between the recirculating volume and the free-stream flow results in the eddy being ejected into the free-stream flow at 8 cm s^{-1} (Fig. 5E). At this velocity, water within the eddy was fully mixed with the free-stream flow, although particles were still seen to circulate within the undulation for a short time (Fig. 5E). Flow around and within the smaller undulation on the left was similar to that described for the large eddy, but the steep, high, downstream edge of the smaller undulation resulted in a more three-dimensional structure.

Vertical profiles of horizontal velocity along the undulate centerline of the entire sheltered blade used in the June experiments were constructed at bulk flow velocities of 0.5, 1, and 4 cm s^{-1} (Fig. 6). Figure 6 illustrates how the flow field would move dye streaks injected normal to the flow (indicated by the dashed vertical lines along the blade) in a given time. The thickness of the velocity gradient region decreased with increasing free-stream velocity. Owing to varying pressure gradients along the blade surface (*see discussion*), VBLs are thinner along the rising portion of each undulation compared to the falling portion and base regions. Separation behind the last major undulation at 32 cm occurred at the lowest free-stream velocity used (0.5 cm s^{-1}), indicated by the initially steep velocity gradient that rapidly shallows at 35 cm (Fig. 6A). At 1 and 4 cm s^{-1}, recirculation within the separated region behind the last undulation is apparent and indicated by the fluctuating velocity profiles at 40 (Fig. 6B) and 41 cm (Fig. 6C). Separation around the smaller undulations with maximum heights located at 2 and 19 cm is apparent at free-stream velocities of 1 and 4 cm s^{-1} (Fig. 6B,C).

Spines were apparent in the June blade edge experiment but, as for the exposed blade morphology, they had no obvious effect on seawater flow. The small contribution of the bulb to the total frontal area of the sheltered blades meant that this feature had no significant effect on the downstream VBL structure when compared to the edge undulations. In February, the whole sheltered blade flapped at free-stream velocities >8 cm s^{-1}.

Discussion

Boundary layer processes for M. integrifolia—Flat-plate boundary layer theory is typically used to quantify and characterize boundary layers around aquatic plants (e.g. Wheeler 1980, 1988; Koch 1994). However, without even considering that this theory is based on an infinitely wide plate, it is clear that neither wave-sheltered nor exposed blade morphologies of *M. integrifolia* resemble the smooth, flat plate for which this theory was originally developed. Results presented here negate the use of flat-plate boundary layer theory to describe flow around *M. integrifolia.* Separation was the dominant flow pattern around the sheltered blade morphology of *M. integrifolia,* whereas the observed VBL thickness along the exposed blade was greater than that predicted using either laminar or turbulent boundary layer theory. We suggest that seawater flow around both *M. integrifolia* blade morphologies is better described by separation than by flat-plate boundary layer theory.

The sheltered blade morphology of *M. integrifolia* can be considered a curved body. In contrast to a flat plate, the VBL thickness along a curved body varies owing to changing pressure gradients (Denny 1988). When water moves up the rising portion of an undulation, velocity increases and VBL thickness decreases. As water moves down the falling portion of an undulation, velocity decreases and the thickness of the VBL increases rapidly. If the adverse pressure gradient is weak, then flow will not separate, but becomes vulnerable to a premature transition to turbulence at velocities half those found for no imposed pressure gradient (Schlichting 1979). If the adverse pressure gradient is strong, however, the VBL separates from the blade when the momentum flux from the outer flow in not enough to counteract the deceleration owing to the adverse pressure gradient. This was observed at free-stream velocities as low as 0.5 cm s^{-1} for sheltered blades of *M. integrifolia.*

Our experiments were conducted in an experimental system in which the kelp blades were aligned to unidirectional, initially laminar free-stream flow. Although this was necessary to determine how blade morphology affected seawater flow, it is clearly not representative of nature. The nearshore coastal region can be considered a turbulent fluid due to physical forcing by wind, waves, bottom friction, coastal circulation, and tides (e.g. *see* Csanady 1973). In situ dye studies at the Dixon Island sheltered site on a calm summer day (June 1993) indicated rates of spread of a dye cloud of similar initial size to that of a kelp blade were comparable to in situ advection rates (C. L. Stevens et al. unpubl.). Future studies of transport across the DBL might consider the effects of varying turbulence, due to physical forcing, on the VBL structure.

Large-scale separation was not apparent for exposed morphologies of *M. integrifolia* in these laboratory experiments because the blades were pinned to a flat plate and could not hang freely. However, in the field the back-and-forth motion from wave action means that the exposed blades are unlikely to be aligned to the instantaneous seawater flow, which would result in whole-blade separation (C. L. Stevens and C. L. Hurd in prep.). Additionally, close packing of kelp at the exposed site means that only the most upstream blades will experience the free-stream turbulence levels and all subsequent blades must be experiencing the wakes of other blades (C. L. Stevens and C. L. Hurd in prep). At the exposed site, therefore, whole blade separation and a turbulent VBL are predicted.

Functional roles of M. integrifolia *blade morphology*—Our observation that the transition to turbulence for *M. integrifolia* occurs at a Re lower than those predicted from flat-plate boundary layer theory agrees with that of Wheeler (1980). However, our results do not support the hypothesis that *M. integrifolia* from a sheltered site evolved a blade morphology that "trips" a laminar VBL boundary to turbulence at lower velocities than those from a wave-exposed site, because the transition from laminar to turbulent flow occurred at similar free-stream seawater velocities for both morphologies. In retrospect, this result is not surprising because both wave-sheltered and exposed morphologies have similar dimensions and the transition to turbulence will therefore occur at a similar Re; the transition from a laminar to turbulent VBL will occur at similar free-stream velocities for any seaweed with blade dimensions approximating those of *M. integrifolia.*

Although the transition to turbulence occurred at similar free-stream velocities for both *M. integrifolia* blade morphologies, the way in which seawater flowed around blades was clearly different. Recirculating eddies formed in the large edge undulations of the sheltered morphology at seawater velocities up to 4 cm s^{-1}, which is precisely the velocity range over which diffusion-limited ion transport occurs for *Macrocystis* sp. (e.g. Wheeler 1980; Hurd et al. 1996). Because undulating (ruffled) edges are a common feature of kelps growing in wave-sheltered environments (e.g. *Nereocystis luetkeana, Laminaria saccharina, Laminaria longicruris*) compared to the relatively flat edges of wave-exposed kelps (Gerard and Mann 1979; Gerard 1987; Koehl and Alberte 1988), it is tempting to speculate that there is a functional advantage to generating recirculating eddies with regard to nutrient acquisition in low-velocity environments. When the rates of nitrate and ammonium uptake were compared for wave-sheltered and exposed blades of *M. integrifolia,* however, there was no difference in uptake rate per unit surface area (Hurd et al. 1996). We suggest, therefore, that undulations do not function to enhance nutrient acquisition.

Edge undulations may allow wave-sheltered blades to flap at low seawater velocities, thereby "shaking off" any thick DBLs that form. Koehl and Alberte (1988) tested this hypothesis with whole *N. luetkeana* blades and found that the average speed of flapping was similar for both sheltered and exposed morphologies and that flapping was not recorded at free-stream velocities <10 cm s^{-1} (Koehl and Alberte 1988). Similarly, flapping was observed for the sheltered blade morphology of *M. integrifolia* at seawater velocities >8 cm s^{-1}, but not at the lower velocities at which diffusion-limited nutrient transport occurs.

Undulations separate individual blades of *N. luetkeana* in a slow current (10 cm s^{-1}), permitting higher photon flux densities to reach lower blades (Koehl and Alberte 1988). Undulations of *M. integrifolia* are unlikely to perform a similar function, however, because blades of this species are naturally separated along the frond. An alternative idea is that the edge undulations increase drag, which would stretch blades out at the lowest free-stream velocities. This effect would maintain blades perpendicular to incident light, which would be advantageous for photon capture.

In our experimental configuration, the bulb of *M. integrifolia* was the first structural element that seawater encountered, and for the exposed blades it was the main feature affecting seawater flow. However, the primary role of bulbs is clearly to buoy blades up in the water column rather than to generate turbulence. The larger bulbs of the wave-exposed blades may maintain the fronds in a vertical position under high seawater velocities. Similarly, marginal spines of *M. integrifolia* have been described as turbulence-inducing spoilers (Norton et al. 1982). The observation that spines of *M. integrifolia* often grow flush to the blade of exposed plants but arise at irregular angles of sheltered plants lends support to this idea (Pace 1972). However, the extremely small contribution of the spines to overall turbulence observed in our experiments suggests that a role in generating turbulence is unlikely.

Another feature that generally differs between wave-sheltered and exposed blades of *M. integrifolia* is the number of surface corrugations, which may increase surface roughness and thereby increase turbulence at the blade surface (Neushul 1972; Gerard and Mann 1979; Wheeler 1988). To enhance surface roughness, however, the roughness elements need to be of comparable size to the thickness of the VSL of the VBL. Increased surface roughness of seagrass blades from epiphyte settlement has been demonstrated (Koch 1994). However, corrugations of *M. integrifolia* are not at a scale where they effect hydrodynamic roughness and the viscous sublayer will conform to the corrugations. Instead, corrugations may reduce drag at the blade surface, which is of primary importance at wave-exposed sites. Longitudinal grooves (riblets) similar to the surface corrugations of *M. integrifolia* (0.5 × 0.45 cm) reduce frictional drag 7–8%

(compared to a smooth surface) by reducing span-wise vortices and hence turbulence within the riblet valleys (Djenidi et al. 1994). Corrugations may also increase strength while maintaining a relatively high surface area-to-volume ratio (Hurd et al. 1996).

Mechanical stress (in the form of a weight hanging from the end of the blade) triggers the formation of wave-exposed morphologies of *L. saccharina* and in the absence of mechanical stress a wave-sheltered morphology formed (Gerard 1987). For *Egregia menziesii,* mechanical stress stimulated an increase in inorganic carbon uptake and the allocation of fixed carbon to cell-wall synthesis (Kraemer and Chapman 1991). If drag forces similarly trigger the formation of the wave-exposed blade morphology of *M. integrifolia,* it follows that the undulate sheltered morphology forms in conditions where drag forces are below a certain critical value. Whether the undulate kelp blade morphology frequently observed at wave-sheltered sites represents an adaptation to low-velocity environments requires further investigation.

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