

## Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies

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### Abstract

A number of species of macroalgae possess a flat, strap-like blade morphology in habitats exposed to rapidly-moving water whereas those at protected sites have a wider, undulate blade shape. We have explored the functional consequences of flat, narrow vs. wide, undulate blade morphologies in the giant bull kelp *Nereocystis luetkeana*. Our study focused on the behavior of blades in ambient water currents and the consequences of that behavior to breakage and to photosynthesis. In flowing water, the narrow, flat blades flap with lower amplitude and collapse together into a more streamlined bundle than do wide, undulate blades, and hence experience lower drag per blade area at a given flow velocity. If the algae at current-swept sites had ruffled blades, drag forces would sometimes be sufficient to break the stipes. However, flat blades in a streamlined bundle experience more self-shading than do undulate blades, which remain spread out in water currents. Thus, there is a morphological trade-off between reducing drag and reducing self-shading. Photosynthetic <sup>14</sup>C-HCO<sub>3</sub> uptake rates decrease in slow flow when the boundary layer along the blade surface across which diffusion takes place is relatively thick. However, blade flapping, which stirs water near the blade surface, enhances carbon uptake rates in slow water currents for both the undulate and the flat morphologies.

### Introduction

Although many species of macroalgae have blades with undulate edges, the functional consequences of these ruffles have not been demonstrated. A number of species of macroalgae, such as *Hedophyllum sessile* and several *Laminaria* spp., have flat, narrow blades when they occur at sites exposed to rapidly-moving water, but have undulate, wide blades at protected sites (e.g. Sundene 1964, Russell 1978, Gerard and Mann 1979, Kain 1979, Armstrong 1982). We

have explored some of the functional consequences of these two blade morphologies of the giant bull kelp *Nereocystis luetkeana* (Mertens) Postels and Ruprecht. *N. luetkeana* forms extensive beds along the Pacific coast of North America, from California to Alaska. Its blades, which can be up to 4 m long, are held near the water surface by a gas-filled pneumatocyst atop a long, slim stipe attached to the substratum by a holdfast (Abbott and Hollenberg 1976). *N. luetkeana*, which occur in water about 3 to 17 m deep, are exposed to tidal currents as well as to non-breaking waves and surface chop. Deformations of a bull kelp in such flow are diagrammed in Koehl (1984).

Which aspects of the performance of a seaweed in moving water are likely to be affected by the morphology of its blades? When in moving fluid, sheet-like structures (such as flags or algal blades) tend to be carried to an orientation parallel to the direction of fluid movement. They may also flap in the flow. A group of such blades attached to one stipe may be pushed together into a clump by the moving fluid. The extent to which these various reconfigurations occur might influence the likelihood that an alga will be broken by moving water and might limit or promote its photosynthetic performance.

Most seaweeds, such as *Nereocystis luetkeana*, die when they are torn from the substratum by moving water and cast ashore (Koehl and Wainwright 1977). Such breakage occurs when the hydrodynamic force on the seaweed exceeds the breaking strength of its stipe or holdfast (for a review, see Koehl 1986). The drag force on an algal blade is due both to skin friction and to form drag (Hoerner 1965, Batchelor 1967, Vogel 1981). When a fluid moves past a solid object, the layer of fluid immediately next to the solid surface does not slip with respect to that surface. Therefore, a shear gradient (known as the boundary layer) develops in the fluid between the surface of the body and the mainstream flow. The viscous resistance of the fluid to being deformed in shear subjects the body to a force called "skin friction", which tends to move the body downstream. In addition, a wake forms on the downstream side of a large organism

(such as a macroalga) in rapidly-moving fluid. Such organisms are subjected to a net downstream pressure called "form drag". The larger the wake that forms behind a body at a given velocity, the greater the form drag. The greater the velocity of flow, the higher the total drag force. Streaming out parallel to the flow should reduce form drag, whereas flapping should increase it. Clumping together by blades in flow should reduce drag by reducing water velocity across surfaces of some of the blades in the middle of the clump, and by presenting a relatively streamlined bundle to the current. How, then, does blade morphology affect flapping, clumping, and hence drag on a seaweed?

The behavior of algal blades in flowing water might also influence photosynthetic performance, both by affecting the spatial arrangement of the blades with respect to incident radiation, and by altering the rate at which dissolved substances in the water are moved to and from the surfaces of the blades.

Although the photon flux density encountered by *Nereocystis luetkeana* blades might be increased when flowing water carries them up parallel to the water surface, the clumping together of blades that occurs in flow might lead to self-shading. Light attenuation by algal thalli not only reduces the total quantum flux passing through the tissue, but also alters the spectral distribution of that light (e.g. Lüning 1979). Both of these features can have major consequences for photosynthesis and whole-plant production. How does blade morphology affect the degree of self-shading experienced in such bundles, and consequently blade photosynthesis?

Since algal blades take up carbon to support photosynthesis and release dissolved organics and oxygen at their surfaces, diffusion of dissolved materials across the boundary layer of slowly-moving water along the surfaces of blades can limit photosynthesis. Shear gradients along algal blade surfaces are steeper, and hence photosynthetic rates are higher, the faster the flow; however, above some water-velocity saturation point, diffusion is no longer limiting to photosynthesis (for a review, see Koehl 1986). If flow along the surface of an algal thallus is turbulent, mass and momentum are transferred across the boundary layer in eddies and photosynthetic rate can be increased. Morphological features of algae that have been suggested as introducing turbulence near blade surfaces, and thus enhancing photosynthesis, include rugosities, perforations, marginal spines, and floats (that cause fronds to be carried up and down in waves) (Neushul 1972, Wheeler 1980a, 1980b, Norton et al. 1981, Gerard 1982). How do ruffles affect flow near blades?

To explore the functional consequences of undulate blade morphology, we compared the performance in moving water of flat *Nereocystis luetkeana* blades with that of undulate ones. As the discussion above suggests, such a study should include a diverse set of measurements. First, the water flow habitats of undulate vs. flat blades should be characterized, and the morphological differences between the two blade shapes should be quantified. Then the flapping and the clumping behavior of the two blade morphs in moving water should be measured. The consequences of this

blade behavior to susceptibility to breakage in flowing water can then be investigated by quantifying hydrodynamic forces on and mechanical strengths of *N. luetkeana* of both morphs. In addition, the effects of blade behavior on self-shading and on uptake of dissolved substances should be assessed to explore consequences to the photosynthesis of blade shape.

## Materials and methods

### Field sites and water flow

*Nereocystis luetkeana* (Mertens) Postels and Ruprecht was studied from two sites near San Juan Island, Washington. The "protected" site was a stretch of shore between Shady Cove and Cantilever Point near Friday Harbor Laboratories, and the "current-swept" site was Turn Rock in the San Juan Channel.

Current velocities encountered by *Nereocystis luetkeana* blades at these two sites were measured in May 1975 using an EPCO Model 6130 electromagnetic flowmeter, in June and July 1982 using a Marsh-McBirney Model 511 electromagnetic flowmeter and in October 1981 using a Marsh-McBirney Model 523 electromagnetic flowmeter. Signals from the flowmeters were recorded on magnetic tape as described by Koehl (1977). Water flow relative to the sensor should be the same as that relative to the *N. luetkeana* blades, which are supported by a tethered float rather than a rigid stalk. So that our flow probe would move with the kelp, we mounted it on a metal arm extending from a small boat tied by a short length of rope to *N. luetkeana* pneumatocysts. We observed no noticeable motion of the boat relative to the kelp. The probe was positioned at the depth of the nearest *N. luetkeana* blades, usually 10 to 50 cm below the water surface. Because our sites were exposed to tidal currents rather than wave action, we oriented the probe to measure the x and y (horizontal) components of velocity. Moving a probe vertically did not alter the x and y signals, hence we assumed that the slight up-and-down motion the boat sometimes underwent did not impose artifacts on the flow records.

The kelp bed at the protected site was only a few meters wide, so flow was recorded in the middle of the bed at a number of positions along the shore. The kelp bed at the current-swept site was expansive, hence flow was recorded at several positions, some a few meters from the edge of the bed and others in the middle of the bed. Flow at the protected site was recorded throughout the tidal cycle; flow at the current-swept site was recorded from slack tide until the tidal current grew so swift that we could not hold the boat and probe steadily. Consequently we have no records of the peak velocities at that site.

### Morphometrics

*Nereocystis luetkeana* were collected for morphometric analysis from the edge and middle of the current-swept kelp bed

and from the protected kelp bed described above during the spring of 1975, the autumn of 1981, and the summer and autumn of 1982. A position in the kelp bed was chosen haphazardly, and all the plants within reach of that position were collected. Diameters of stipes were measured to the nearest mm using vernier calipers. All the blades on a plant were removed, spread out along with grids marked in cm, and photographed from an overhanging balcony one story above them. Measurement of the grids at various positions on each photograph was controlled for parallax. These slides were projected onto paper, the blade widths measured to the nearest mm, and the blade perimeters traced. The projected areas of the blades were measured to the nearest 0.01 m<sup>2</sup> by weighing the paper cut-outs of the tracings. The real area of a ruffled blade is greater than its projected area. Therefore, after photographing intact blades to measure the projected area, we cut the blades into pieces that would lie flat, photographed them, and measured the real area by weighing the paper cut-outs as described above.

#### Measurement of drag

Drag force on individual *Nereocystis luetkeana* was measured (Koehl and Wainwright 1977, 1985) to the nearest 0.1 N using an Ametek Model LKG5 force gage or an Ohaus spring scale. Each plant was towed just below the water-surface at a number of different velocities (measured with a Marsh-McBirney Model 511 or 523 electromagnetic flowmeter) outside the wake of a boat. We focused on velocities at the high end of the range encountered in situ to examine susceptibility of plants to breakage by currents. All the blades of some undulate kelp were removed and used as patterns to cut out flat plastic models of the blades. These model blades were attached to the pneumatocyst of the plant and drag was measured as described above.

#### Measurement of flapping

The vertical flapping amplitude of individual blades of *Nereocystis luetkeana* was measured in a flow tank (Vogel and LaBarbera 1978) with a working section 1 260 cm<sup>2</sup> in cross-sectional area. Only blades 1 m in length (mature blades whose distal ends had broken off, by appearances, after the release of sori) were used so that they would fit in the region of the tank with even flow. Each blade was attached at its proximal end to a horizontal wire across the middle of the upstream end of the working section of the tank; the trailing end of the blade was free to move. As a blade flapped up and down in moving water, its highest and lowest positions at a point 70 cm from its attached end were measured by sighting along centimeter grids on the front and back walls of the flow tank. A stopwatch was used to measure to the nearest 0.01 s the durations of cycles of flapping.

#### Measurement of clumping

The maximum width of a clump of blades on a *Nereocystis luetkeana* was measured to the nearest centimeter as the

plant was towed under a platform with a grid on it near the water surface. Kelp were towed from an adjacent dock, and velocity was determined by measuring, with a stopwatch to the nearest 0.1 s, the time required for the plant to travel 13.40 m. Velocities were in the same range as those used for drag measurements, so that we could relate clump width to drag. Similar measurements were made on kelp bearing flat plastic models of their blades (described above). The widths of all the blades on each kelp were measured at intervals along their length. Plants from the current-swept site generally had more blades ( $\bar{x}=42$  blades/plant,  $SD=17.3$ ,  $n=14$ ) than those from the protected site ( $\bar{x}=19$  blades/plant  $SD=7.4$ ,  $n=19$ ). Plants for the clumping experiments, and for the drag experiments involving models, were chosen to have numbers of blades within 12% of the mean for their site.

#### Measurement of strength

The tensile breaking strengths (force per cross-sectional area required to break them) of pieces of *Nereocystis luetkeana* stipes were measured by conducting stress-strain tests using the techniques described by Koehl and Wainwright (1977). These tests were conducted on a Houndsfield Tensometer, Model W, set up as described by LaBarbera (1985). Strengths were measured for plants collected at the protected and the current-swept sites as described above. Tests were done on three replicate specimens per stipe, and strengths were only calculated for specimens that did not slip or break at the tensometer grips. When more than one test was successful for a stipe, we used the mean strength value for that plant.

#### Photosynthesis determination

The effects of photon flux density, water flow, and flapping on the photosynthetic rates of strips of *Nereocystis luetkeana* blades were measured. Kelp were collected at Cantilever Point, flown on ice to Woods Hole, Massachusetts, and maintained in running seawater at 14° to 16°C for 1 to 3 d prior to experimentation. The photosynthetic rate of *N. luetkeana* varies as a function of season (Wheeler et al. 1984), hence all kelp were collected on one day in mid-summer. Strips of blade from three different plants were exposed to each treatment. Since the photosynthetic rates of different regions of a blade might differ (Wheeler et al. 1984, Arnold and Manley 1985), all samples were taken from the middle of non-reproductive regions of the blades, about 50 cm from the pneumatocyst. Strips were cut from the blades immediately before an experiment and washed repeatedly in ultra-filtered (0.2 μm) seawater until mucilage exudation ceased. This treatment also eliminated any "wound response" in the tissue respiratory behavior (Alberte unpublished data).

Photosynthesis vs irradiance (P-I) relationships of *Nereocystis luetkeana* blade discs (1.25 cm<sup>2</sup>) were measured using a Clark-type oxygen electrode (Rank Brothers) as

described by Dennison and Alberte (1982). The tissue chamber was maintained at  $14^{\circ}\text{C} \pm 1^{\circ}\text{C}$  using a circulating water bath, and a range of photon flux densities were obtained using neutral density screening and a Kodak projector lamp (500 W) as a light source. Photon flux densities (PAR, photosynthetically active radiation) were measured using a Biospherical QSL-140 (Biospherical Instruments)  $4\pi$  integrating quantum sensor. Rates of dark respiration were also determined. The value of  $I_k$ , the photon flux density at which photosynthesis saturates, was determined at the intersection of the regression lines of the initial slope and  $P_{\max}$  (Dennison and Alberte 1982).

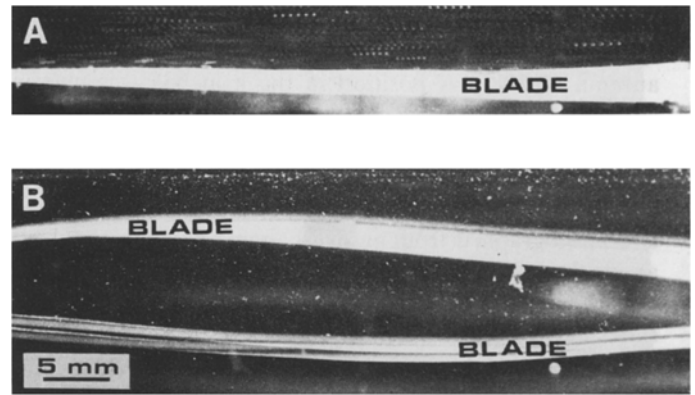
Photosynthetic rates of strips of *Nereocystis luetkeana* blades in a flow tank were measured using  $^{14}\text{C}$ -bicarbonate (Mazella and Alberte 1986). Each strip ( $1 \times 12$  cm) was held in the middle of a recirculating flow tank (Vogel and LaBarbera 1978) of  $9\text{ cm}^2$  cross-sectional area by a horizontal thread across the width of the tank at the leading edge of the strip and a vertical needle to the trailing edge. This needle could be moved up and down by an electric motor to flap the strip at a frequency of 1 to 3 Hz and an amplitude of 2 cm. Water in the flow tank was kept at  $14^{\circ}$  to  $16^{\circ}\text{C}$  with an ice jacket. After being mounted in the flow tank in ultrafiltered ( $0.2\ \mu\text{m}$ ) seawater, strips were allowed to acclimate to the flow and light conditions for at least 15 min prior to the addition of  $^{14}\text{C}$ - $\text{NaHCO}_3$ . Experiments were conducted at  $14^{\circ}$  to  $16^{\circ}\text{C}$  for 1 h with photon flux densities of  $630 \pm 5\ \mu\text{E m}^{-2}\ \text{s}^{-1}$  (PAR). These levels were above photosynthetic saturation. Dark controls were also run for each blade under each flow treatment. Tissue was killed and digested in Protosol (NEN) for 16 h at  $50^{\circ}\text{C}$  to fully oxidize the sample and to minimize quenching due to chlorophyll. Econofluor (NEN) was used as the scintillation cocktail. The chlorophyll  $a+c$  content of blade tissue cut immediately adjacent to the strips used for photosynthesis determination was measured in 90% volume ratio (v/v) acetone extracts using the equations of Jeffrey and Humphrey (1975).

#### Photon flux density in the field

The  $4\pi$  quantum sensor described above was used to measure photon flux densities of PAR encountered by *Nereocystis luetkeana* at our two field sites. Integrated light samples for 60 s each were taken at different times during sunny and cloudy days. Photon flux density was measured in water at the depth of *Nereocystis luetkeana* blades: (1) with no blades over the sensor, (2) with various numbers of blades held over the sensor, and (3) with unrestrained blades of one plant over the sensor. In the latter case, kelps with strap-like blades and kelps with ruffled blades were used in a variety of water-flow conditions, which were measured as described above.

#### Characterization of water flow in uptake experiments

Mainstream velocities in the middle of the flow tank when no strips were present were measured by adding neutrally-buoyant particles to the water and using a stopwatch to time



**Fig. 1.** *Nereocystis luetkeana*. Long-exposure photographs of strobotac-illuminated neutrally-buoyant particles carried in water moving from right to left past strips of blade in flow tank. The closer together the dots in a row, the slower the flow at that position. (A) Stationary blade strip. (B) Blade strip flapping up and down (shown in several positions as it was illuminated by successive flashes of the strobotac)

their travel across measured distances. Experiments were run at two mainstream velocities ( $4.3 \times 10^{-3}$  and  $8.5 \times 10^{-3}\ \text{m s}^{-1}$ ), chosen to be well below the saturation velocities for nitrogen uptake measured for other kelp ( $2.5\text{--}4 \times 10^{-2}\ \text{m s}^{-1}$ , Wheeler 1980 a, Gerard 1982).

Water velocity profiles along strips of *Nereocystis luetkeana* blades were measured for each of the water speeds used in the flow tank. Particles were added to the water and those in a vertical plane at the middle of the tank were illuminated by a strobotac (GenRad Model 1531-A) shining through a slit in an opaque panel above the tank. The bright dots in long-exposure photographs, as shown in Fig. 1, indicate the positions of particles during successive flashes of the strobotac. The product of the frequency of strobe flashing and the distance between successive dots gives the velocity of the water at the position of the dots.

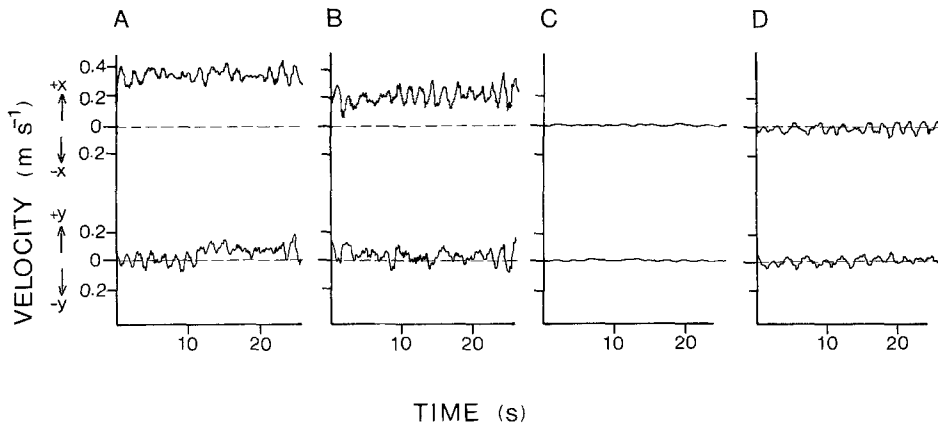
The steeper the shear gradient in the water flowing along a blade, the greater the rate of mass transfer to the blade surface of substances being depleted from the water at the blade surface. The measure we used for the steepness of this shear gradient was analogous to the boundary shear velocity ( $u_*$ ) used to describe fluid flow along the substratum (see e.g. Monteith 1973). We used our measurements of velocity profiles to calculate  $u_*$  for each of the mainstream velocities employed in our experiments as follows:

$$u(z) = (u_*/K) \ln [(z-d)/z_0],$$

where  $u$  = velocity,  $K$  = von Karman's constant (0.4),  $z$  = height above the blade surface,  $d$  = the height that the logarithmic boundary layer is elevated above the surface, and  $z_0$  = the roughness height of the surface. We ignore  $z_0$  and take  $d$  to be zero in the case of a smooth strip of algal blade.

#### “Boundary shear velocity” along blades of different morphologies

Rough estimates of average shear velocities along surfaces of blades of different morphologies exposed to the same



**Fig. 2.** *Nereocystis luetkeana*. Examples of water flow encountered by blades in situ. The +x indicates horizontal flow velocity in one direction, -x indicates horizontal flow velocity in opposite direction, and +y and -y indicate horizontal flow velocity simultaneously recorded at right angles to x-axis. The +x velocity in (A) and (B) is in direction blades of kelp were streaming. (A) Current-swept site, edge of kelp bed, ca. 2 h after slack low tide on windy day. (B) Current-swept site, middle of kelp bed, ca. 1.5 h after slack tide on same day as (A). (C) Current-swept site, middle of kelp bed, at slack tide on non-windy day. (D) Protected site, slack tide on windy day

field conditions were made by measuring the weight loss during a 10 min interval of candy (Life Savers) sewn to blades. This technique is akin to Gerard's (1982) use of plaster buttons to measure flow along the blades of *Macrocystis pyrifera*. Blades on intact *Nereocystis luetkeana* were lifted out of the water and blotted; "Pep-o-mint" Life Savers were sewn to them with four loops of thread at measured positions. The plants were then hung from the floating dock at Friday Harbor Laboratories during slack tide on windy days (flow conditions similar to those shown in Fig. 2D). After 10 min blades were lifted from the water and the Life Savers quickly removed, dried, and weighed. Life Savers were calibrated by sewing them to stiff plastic sheets that were then attached to the floor of a flow tank in which known  $u_*$ 's could be produced. Three replicate calibrations were done at each of three  $u_*$ 's, and measurements were found to be repeatable to the nearest  $5 \times 10^{-4} \text{ m s}^{-1}$ .

**Results and discussion**

**Water flow habitats**

Examples of horizontal water velocities encountered by *Nereocystis luetkeana* blades are shown in Fig. 2. The water movement is a combination of surface chop (due to wind and the wakes of passing boats) superimposed on tidal currents. Therefore, on breezy days the flow past *N. luetkeana* blades is characterized by rapidly-fluctuating velocity (Fig. 2A, B, D). In contrast, at slack tide on non-windy days, water near the kelp blades can be quite still (Fig. 2C).

Several aspects of such flow patterns are important to the biology of the kelp. Hydrodynamic forces can break kelp stipes; the greatest mechanical loads that stipes must withstand depend on the peaks of water velocity. Flowing water also carries dissolved substances to and from the kelp. Mean flow velocity gives a measure of the average unidirectional flux of water past the blades (i.e., advective transport), whereas turbulence intensity indicates the importance, relative to this advective transport, of rapid small-scale water motions that may lead to local mixing. [Turbulence intensity, which is a measure of the importance of velocity fluctuations relative to the average current, is given by  $(\overline{u'^2})^{1/2}/\bar{u}$ ,

**Table 1.** *Nereocystis luetkeana*. Examples of mean velocities and turbulence intensities<sup>a</sup> encountered on windy days

Location and time	Velocity ( $\text{m s}^{-1}$ )		Turbulence intensity <sup>a</sup> ( $\text{m s}^{-1}$ )
	maximum	mean	
Current-swept site			
edge of bed, ~1 h after slack tide <sup>b</sup>	0.49	0.33	0.21
middle of bed, ~1 h after slack tide <sup>b</sup>	0.39	0.22	0.29
middle of bed, slack tide <sup>b</sup>	0.12	0.004	10.64
Protected site			
peak tidal current	0.57	0.36	0.22

<sup>a</sup> Turbulence intensity was calculated from velocities taken at 0.5 s intervals ( $n=256$  per record) on records of flow like those shown in Fig. 2

<sup>b</sup> Low, low water

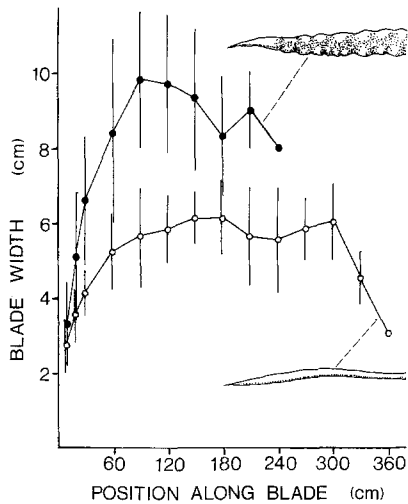
**Table 2.** *Nereocystis luetkeana*. Examples of ranges of velocity encountered 1 h after slack low tide

Location	Windy day ( $\text{m s}^{-1}$ )	Calm day ( $\text{m s}^{-1}$ )
Exposed site		
edge of bed	0.05 to 0.51	0.31 to 0.42
middle of bed	0 to 0.39	—
Protected site	-0.10 <sup>a</sup> to 0.10	0 to 0.10

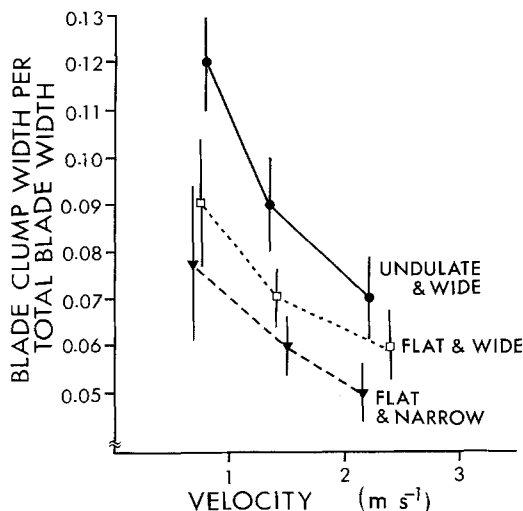
<sup>a</sup> Velocity is a vector having both magnitude and direction. Velocities reported in this table are horizontal in direction of tidal current; negative velocity indicates flow in opposite direction

where  $u'$  = the deviation of the velocity at an instant in time from the mean velocity,  $\bar{u}$  (see e.g. Anderson and Charters 1982)].

Examples of mean water velocity (in the direction of tidal flow) and turbulence intensity are given in Table 1, and examples of ranges of velocities are given in Table 2. These data and Fig. 2 illustrate three important characteristics of the water flow encountered by *Nereocystis luetkeana* at our field sites: (1) Flow at a site can change considerably from one time in the tidal cycle to another, and velocity fluctua-



**Fig. 3.** *Nereocystis luetkeana*. Examples of blade widths on plant from protected site (●) and from current-swept site (○). Blade positions were measured from pneumatocyst. Values plotted represent means for 20 blades on each plant (all blades on protected plant, and all blades in one of bundles of blades on current-swept plant), and error bars represent one standard deviation. Diagrams illustrating proximal end of each blade type were traced from photographs of blades



**Fig. 4.** *Nereocystis luetkeana*. Index of non-clumping (width of the clump of blades on plant divided by total of widths of all blades on that plant) for plants towed at various velocities. Error bars represent one standard deviation about the mean ( $n=3$  in each case) for wide, undulate blades (●), for narrow, flat blades (▼), and for flat plastic models (□) of the wide blades

tions can be increased by wind. (2) Both the peak and the mean velocities measured at the current-swept site are greater than those measured at the protected site at comparable times during the tidal cycle (except at slack tide). For example, ca. 1 h after slack low tide on both windy and non-windy days, flow at the current-swept site was faster than at the protected site (Table 2). During the fastest part of a flooding tide at the protected site, the mean velocity was  $0.36 \text{ m s}^{-1}$ , with a peak of  $0.57 \text{ m s}^{-1}$ . Although we were unable to measure the fastest flooding tidal current at the current-swept site, the Tidal Current Tables (NOAA 1981) report it as  $1.03 \text{ m s}^{-1}$  for that day, and velocity peaks were no doubt higher still. (3) Kelp near the edge of the *N. luetkeana* bed at the current-swept site encountered faster flow than did kelp in the middle of this large bed. This result is consistent with measurements of reduced water flow made in other kelp forests (e.g. Kitching et al. 1952, Jackson and Winant 1983).

### Blade morphology

*Nereocystis luetkeana* from the exposed site had narrower blades than those from the protected site (Fig. 3, Table 3). Further evidence that narrower blades are associated with faster water motion is that blades of plants at the edge of the exposed kelp bed were significantly narrower (mean width = 3.1 cm,  $n=171$ ) than those of plants from the middle of the bed (mean width 4.4 cm,  $n=211$ ) (ANOVA,  $p<0.05$ ; Sokal and Rohlf 1969).

The ratio of the real area of a blade to its projected area is a measure of the degree to which the blade is undulate (i.e., ruffled). The median of this ratio for *Nereocystis luetkeana* blades from the protected site (1.09,  $n=13$ ) was significantly higher than that for exposed blades (1.00,  $n=37$ ) (Mann-Whitney-Wilcoxon Test,  $p<0.001$ , Gibbons 1976).

We suspect that the measured differences in morphology were the result of phenotypic plastic growth responses of the kelp. Reciprocal transplant experiments conducted in 1985, 1986, and 1987 show that flat *Nereocystis luetkeana* become more ruffled when moved to slower flowing currents and that undulate *N. luetkeana* become flatter when moved to faster currents (Koehl and Baron unpublished data). Transplant experiments on other seaweed species reveal similar morphological plasticity (e.g. Sundene 1964, Norton 1969, Gerard and Mann 1979, dePaula and deOlivera 1982).

**Table 3.** *Nereocystis luetkeana*. Characteristics of current-swept and protected kelp

Characteristic	Current-swept $\bar{x}$ (SD, $n$ )	Protected $\bar{x}$ (SD, $n$ )	Significantly different? (Analysis of variance: ANOVA, $p<0.05$ )
Blade width (cm)	3.8 (2.1, 383) (9 plants)	7.8 (3.2, 346) (18 plants)	yes
Stipe diameter (mm)	6.0 (2.6, 9)	5.3 (1.5, 18)	no
Stipe breaking stress ( $\text{MN m}^{-2}$ )	2.9 (0.7, 9)	2.7 (2.1, 18)	no
Drag per blade area at $0.5 \text{ m s}^{-1}$ ( $\text{N m}^{-2}$ )	3.2 (1.5, 9)	13.4 (6.8, 18)	yes

### Behavior of blades in moving water

Narrow, flat blades on a *Nereocystis luetkeana* in moving water clump together into narrower bundles than do wide, undulate blades (Fig. 4). To test whether the undulate edges alone were responsible for this difference in clumping behavior, we compared the clump width of wide undulate blades with that of models of those blades. The blade models were of the same dimensions as the real blades but were flat. As shown in Fig. 4, clump width for the models was intermediate between that of wide undulate blades and that of narrow, flat blades. This indicates that both the narrowness and the flatness of the current-swept blades contribute to their ability to clump together into narrow bundles in moving water.

Measurements of up-and-down motion of individual blades in the flow tank indicate that wide, undulate blades flap with greater amplitude and larger variation in amplitude than narrow, flat blades (Fig. 5). However, because the flat blades flap at higher frequencies than the undulate ones, the average speed of up-and-down movement of the two morphs is rather similar. We measured flapping of individual blades 1 m long in the flow tank (where turbulence was minimized) so that the behavior of the different morphologies under the same flow conditions could be compared. Therefore, we have not quantified how blade length, neighboring blades on the same plant, or different levels of turbulence affect flapping behavior, nor have we quantified flapping behavior at velocities greater than the maximum ( $0.5 \text{ m s}^{-1}$ ) of the flow tank. We have noticed, however, that when plants are towed in the field at the same velocities (up to  $2.5 \text{ m s}^{-1}$ ) under the same conditions of surface chop, those with ruffled blades flail around whereas those with strap-like blades flutter gently.

### Drag and breakage

Drag force per blade area is greater for wide, undulate blades than for narrow, flat ones (Table 3). This result is not surprising since drag depends upon wake size, which is smaller for the strap-like blades that flap with lower amplitude and that collapse into narrower, more streamlined bundles than ruffled blades. Comparison of drag on model blades with that on real ones (Fig. 6) suggests that both the undulate edges and the greater width of protected blades contribute to their higher drag per blade area.

When *Nereocystis luetkeana* are ripped off the substratum, they often break at the stipe (Koehl and Wainwright 1977). Therefore, to evaluate the hydrodynamic force that a *N. luetkeana* can bear, we measured the diameters and breaking strengths of stipes. We found that kelp from our two field sites did not differ significantly in these traits (Table 3).

Would the kelp at the current-swept site be in danger of breaking if they had wide, ruffled blades rather than narrow, flat ones? Consider the example of a kelp from the current-swept site (the individual illustrated in Fig. 6) with a total blade area of  $4.1 \text{ m}^2$ . If this kelp had wide, undulate blades rather than slim, flat ones, the drag on the entire plant in a

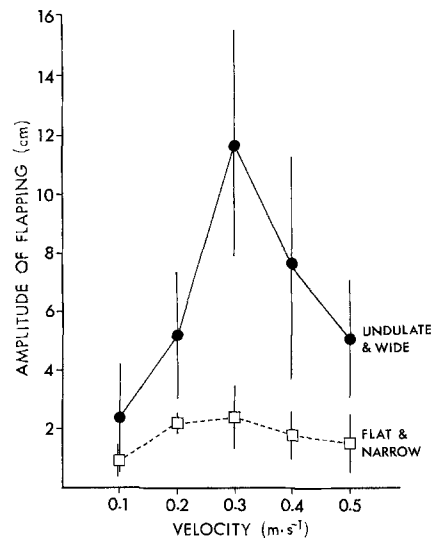


Fig. 5. *Nereocystis luetkeana*. Examples of amplitude of up-and-down flapping of single plant blades in a flow tank at various velocities. Amplitude was measured at a position 70 cm downstream from attached end of each blade. Error bars represent one standard deviation around means ( $n=5$  in each case) for undulate, wide (●) and flat, narrow (□) blades

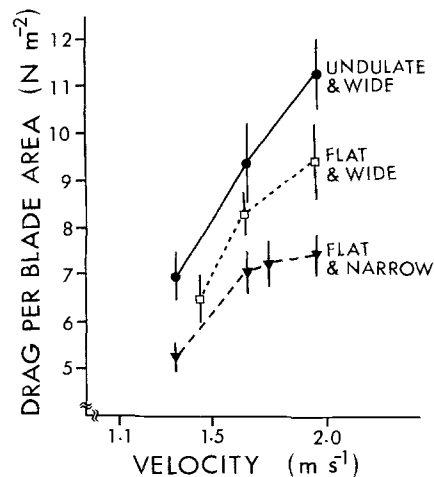


Fig. 6. *Nereocystis luetkeana*. Examples of drag per blade area for plant from protected site with wide, undulate blades (●), for that plant bearing flat plastic models of its blades (□), and for a plant from current-swept site with flat, narrow blades (▼). Error bars represent one standard deviation ( $n=12$  in each case)

$0.5 \text{ m s}^{-1}$  current would be 55 N, and the stress in the stipe would be  $1.9 \text{ MN m}^{-2}$  (calculated using mean values in Table 3). Although this is lower than the mean strength of stipe tissue, some plants do have tissues weak enough to break at such a stress. Furthermore, if the drag per blade area was higher than the mean by one standard deviation, or the stipe diameter lower by one standard deviation (see Table 3), then the stress in the stipe would be 2.9 or  $6.1 \text{ MN m}^{-2}$ , respectively. Although *Nereocystis luetkeana* stipes can bear high loads of very short duration (Koehl and Wainwright 1977), it seems likely that in steady tidal currents of  $0.5$  to  $1.0 \text{ m s}^{-1}$  at the current-swept site, this plant would be in some danger of breaking if it had ruffled blades. We might then interpret the flat, narrow blade morphology as a

drag-reducing feature that permits plants in rapid flow to have large blade areas.

#### Relationship between blade morphology and self-shading

Our measurements of the photosynthetic rate of *Nereocystis luetkeana* blade tissue at various photon flux densities, and measurements made by other investigators (see Wheeler et al. 1984), show that *N. luetkeana* is extremely effective at using low quantum fluxes to drive photosynthesis. We found that the photon flux density at which photosynthesis of *N. luetkeana* blade tissue saturates ( $I_k$ ) is ca.  $110 \mu\text{E m}^{-2} \text{s}^{-1}$ . We also found that photosynthetic compensation is reached at extremely low photon flux densities (ca.  $10 \mu\text{E m}^{-2} \text{s}^{-1}$ ). We found the initial slope ( $\alpha$ ) of the P-I curve to be very steep ( $0.045 \text{ Mol O}_2 \text{ E}^{-1}$ ), with the half-saturation value of photosynthesis achieved at  $60 \mu\text{E m}^{-2} \text{s}^{-1}$ . The maximum photosynthetic rate ( $P_{\text{max}}$ ) we obtained from oxygen evolution measurements ( $5.0 \mu\text{Mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ ) are similar to those obtained from  $^{14}\text{C-NaHCO}_3$  measurements (when compared using the relationship  $g \text{ C} = g \text{ O}_2 / 0.30$ ; see Dennison and Alberte 1985). Our values for  $P_{\text{max}}$ ,  $I_k$ , and  $\alpha$  are similar to (but slightly higher than) those reported by Wheeler et al. (1984) for mid-blade tissue of *N. luetkeana* collected in Canada during the late summer. Interestingly, the  $I_k$  values for many kelp species determined in a variety of geographic regions is usually around  $100 \mu\text{E m}^{-2} \text{s}^{-1}$  (e.g. Wheeler 1980b, Smith et al. 1983; Arnold and Manley 1985, Gerard 1986; Alberte unpublished data), suggesting that kelps and other benthic marine species (e.g. seagrasses, Dennison and Alberte 1985) may not benefit from periods of high quantum flux.

Examples of our measurements of photon flux densities of PAR encountered by *Nereocystis luetkeana* blades in situ are given in Fig. 7 and Table 4. On cloudy days ambient scalar irradiance at midday can be 500 to  $800 \mu\text{E m}^{-2} \text{s}^{-1}$  at the depth of the blades in the water column. Under these conditions, the level of PAR passing through a single blade is less than 50% of ambient PAR, while that passing through two blades is less than 20% of ambient PAR (Fig. 7). Thus, if blades stack up on top of each other, photon flux density levels available to the lower blades can be greatly reduced. However, the consequences of such self-shading on photosynthesis would be minor under midday irradiance levels, even on the cloudy days that often occur in the Pacific Northwest, because the  $I_k$  of *N. luetkeana* is so low. In contrast, ambient PAR levels are considerably lower early and late in the day, and are often well below the  $I_k$  for blade photosynthesis. Under these circumstances, self shading could lead to substantial reduction of the photosynthetic rate. The impact of these reductions on daily carbon balance would be significant (see Dennison and Alberte 1985).

Examples of the effect of water flow on self-shading by *Nereocystis luetkeana* when ambient PAR was below  $I_k$  are given in Table 4. During slack tide, the blades hang down into the water column, leading, for example, to a 70% reduction in PAR beneath the undulate, wide blades of a kelp at the protected site (compared with ambient PAR at the

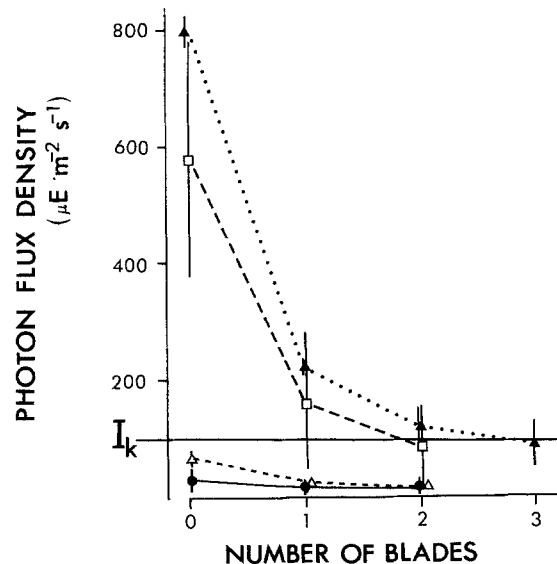


Fig. 7. *Nereocystis luetkeana*. Examples of changes in photon flux densities (PAR) measured in situ at depth of plant blades with increasing numbers of blades held over sensor. Solid horizontal line indicates the  $I_k$  value for blades determined in the laboratory using oxygen evolution technique. Light measurements were made at different times during cloudy days: noon ( $\Delta$  and  $\square$ ), just after sunrise ( $\Delta$ ), and 1 h before sunset ( $\bullet$ ). Each measurement represents average over 1 min. Error bars represent one standard deviation ( $n=3$  for each case)

Table 4. *Nereocystis luetkeana*. Photon flux density of PAR under unrestrained blades in situ as a percent of flux in water column at depth of blades

Blade type	Mean velocity ( $\text{m s}^{-1}$ )	% photon flux density of ambient <sup>a</sup>	
		$\bar{x}$	(SD, $n$ )
Flat, narrow	0.1–0.2	29%	(3, 2)
Undulate, wide	0 (slack tide)	30%	(9, 3)
Undulate, wide	0.1	84%	(23, 4)

<sup>a</sup> Measured on cloudy days when photon flux density of PAR at the depth of the blades was 30 to  $50 \mu\text{E m}^{-2} \text{s}^{-1}$ . Each measurement was averaged over 1 min

same depth without blades nearby). The photon flux densities under these ruffled blades in a current of  $0.1 \text{ m s}^{-2}$ , however, was only reduced by 16%. In contrast, the flat, narrow blades of kelp at the current-swept site are clumped together so much, even by currents as slow at  $0.1 \text{ m s}^{-1}$ , that photon flux density just below them is reduced by over 70%. Comparison of the behavior of flat vs undulate blades in moving water, as discussed above, shows that the ruffled morphology reduces self-shading, not only by keeping the blades spread apart in water currents, but also by increasing the amplitude and variability of blade movement such that the amount of time that one blade is shaded by others is reduced. The latter is likely to be important if *N. luetkeana* can take advantage of fluctuating light, as can terrestrial plants (e.g. Nobel 1979) and other seaweed (e.g. Bidwell et al. 1984, Gerard 1986).



**Table 5.** *Nereocystis luetkeana*. Photosynthetic rates of strips of blades determined at low water velocities in flow tank using  $^{14}\text{C-NaHCO}_3$  when blades were held stationary (no flapping) and when they were flapped up and down (flapping). Value of boundary shear velocity ( $u_*$ ) was determined under non-flapping conditions. Rates are provided on both area and chlorophyll ( $a+c$ ) basis

$u_*$ ( $\text{m s}^{-1}$ )	Photosynthetic rate	
	No flapping $\bar{x}$ (SD), $n=3$	Flapping $\bar{x}$ (SD), $n=3$
Area basis ( $\mu\text{g C cm}^{-2} \text{ hr}^{-1}$ )		
$2.2 \times 10^{-3}$	0.21 (0.018)	0.42 (0.053)
$5.8 \times 10^{-3}$	0.43 (0.073)	0.69 (0.047)
Chlorophyll basis ( $\mu\text{g C mg Chl}^{-1} \text{ min}^{-1}$ )		
$2.2 \times 10^{-3}$	3.00 (0.26)	6.00 (0.75)
$5.8 \times 10^{-3}$	6.15 (1.04)	9.86 (0.67)

### Photosynthesis in slowly-moving water

Examples of the paths of particles in the water next to *Nereocystis luetkeana* blade tissues in the flow tank used for the  $^{14}\text{C-NaHCO}_3$  uptake experiments are shown in Fig. 1. Under these conditions, an increase of boundary shear velocity ( $u_*$ ) leads to an increase in carbon uptake rate (Table 5). Furthermore, at these low velocities, flapping (which stirs up the water as shown in Fig. 1 B) increases photosynthetic rate (Table 5). Such flapping has a more dramatic influence on carbon uptake when the ambient current is slower. These results indicate that the velocities used in the flow tank experiments were below saturation velocity for *N. luetkeana* photosynthesis.

The large effect on photosynthetic rate of the local flow conditions along flapping blade surfaces suggests that caution should be used in interpreting how well field conditions are mimicked in studies using flexible blade enclosures to examine kelp photosynthetic activities in situ (e.g. Gust 1977).

Can slow water flow limit *Nereocystis luetkeana* photosynthesis in the field? Wheeler (1980a) pointed out that water currents within *Macrocystis pyrifera* forests can be below saturation velocities for maximum photosynthesis. In contrast, Gerard (1982) indicated that, because buoyant *M. pyrifera* fronds are moved up and down in waves, the water movement *relative to blade surfaces* in the field can be above saturation velocity even if the ambient current is slow. We worked at sites exposed to tidal currents rather than to heavy wave action, and hence expected that flow-limitation to photosynthesis would be most likely at slack tide. During one windy slack tide, mean  $u_*$  along *N. luetkeana* blades allowed to flap freely was  $5.8 \times 10^{-3} \text{ m s}^{-1}$  ( $n=48$ ), and during another it was  $6.0 \times 10^{-3} \text{ m s}^{-1}$  ( $n=40$ ), as averaged over a 10 min period using the candy-dissolution technique. These estimated  $u_*$ 's are similar to  $u_*$  used in the flow tank, suggesting that at slack tide, even in wind (i.e., ambient velocities as illustrated in Fig. 2 D), water flow can be limiting to photosynthesis. Furthermore, our estimates of  $u_*$  are only for the top blade on each plant (to rule out effects of blade rubbing on weight loss of the Life Savers);  $u_*$ 's along

surfaces of blades in the middle of clumps are likely to be even lower than those we measured.

Does blade morphology, and hence flapping behavior, affect  $u_*$  along blade surfaces during sluggish ambient water motion (when slow flow can limit photosynthesis)? During the two slack tides reported above, even though plants of both morphologies were transplanted to be side-by-side in the same flow conditions, we found no significant differences (ANOVA) in  $u_*$  as a function of position on a blade (i.e., distance from pneumatocyst, and edge vs midline) or as a function of blade morphology (i.e., undulate vs flat). This result seems surprising at first glance, since undulate blades flap with greater amplitude than do flat ones. However, differences in flapping amplitude are small when ambient flow is slow. Furthermore, flat blades flap with greater frequency than do undulate ones, hence the speed of up-down movement for the two blade morphs is similar.

### Conclusions

*Nereocystis luetkeana* have wide, undulate blades in habitats protected from rapid water flow, but narrow, flat ones at more current-swept sites. The flat, narrow blades stack together into streamlined bundles in flowing water, thereby experiencing lower drag, but also more self-shading, than the ruffled, wide blades that flap at greater amplitude and remain more spread out in currents. Thus, there is a trade-off between reducing drag and increasing photosynthetic rate. In slow flow, such as *N. luetkeana* encounter near slack tide, photosynthetic rate might be limited by the flux of dissolved materials to blade surfaces, but the fluttering of blades can stir up water and increase photosynthetic rate. Although blade morphology can affect photosynthesis by *N. luetkeana* via its influence on self-shading, blade shape does not appear to affect shear velocity (and hence uptake of dissolved substances) at blade surfaces when ambient flow is slow enough to limit photosynthesis.

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