

How kelp produce blade shapes suited to different flow regimes: A new wrinkle

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Synopsis Many species of macroalgae have flat, strap-like blades in habitats exposed to rapidly flowing water, but have wide, ruffled “undulate” blades at protected sites. We used the giant bull kelp, *Nereocystis luetkeana*, to investigate how these ecomorphological differences are produced. The undulate blades of *N. luetkeana* from sites with low flow remain spread out and flutter erratically in moving water, thereby not only enhancing interception of light, but also increasing drag. In contrast, strap-like blades of kelp from habitats with rapid flow collapse into streamlined bundles and flutter at low amplitude in flowing water, thus reducing both drag and interception of light. Transplant experiments in the field revealed that shape of the blade in *N. luetkeana* is a plastic trait. Laboratory experiments in which growing blades from different sites were subjected to tensile forces that mimicked the hydrodynamic drag experienced by blades in different flow regimes showed that change in shape is induced by mechanical stress. During growth experiments in the field and laboratory, we mapped the spatial distribution of growth in both undulate and strap-like blades to determine how these different morphologies were produced. The highest growth rates occur near the proximal ends of *N. luetkeana* blades of both morphologies, but the rates of transverse growth of narrow, strap-like blades are lower than those of wide, undulate blades. If rates of longitudinal growth at the edges of a blade exceed the rate of longitudinal growth along the midline of the blade, ruffles along the edges of the blade are produced by elastic buckling. In contrast, flat blades are produced when rates of longitudinal growth are similar across the width of a blade. Because ruffles are the result of elastic buckling, a compliant undulate *N. luetkeana* blade can easily be pushed into different configurations (e.g., the wavelengths of the ruffles along the edges of the blade can change, and the whole blade can twist into left- and right-handed helicoidal shapes), which may enhance movements of the blade in flowing water that reduce self-shading and increase mass exchange along blade surfaces.

Introduction

Many species of benthic macroalgae have different morphologies in habitats exposed to rapidly flowing water than they do at sites that are protected from fast motion of water. One common ecomorphological pattern shown by many species of macroalgae is that individuals in sheltered habitats have wide, thin, ruffled (undulate) blades, while their conspecifics at more exposed sites have narrow, thick, flat blades (reviewed by Norton et al. 1981, 1982; Koehl 1986) (Table 1).

Nereocystis luetkeana

We have been using the giant bull kelp, *Nereocystis luetkeana*, as a system to study the ecomorphology of seaweeds in habitats exposed to different flow

regimes (Fig. 1). Forests of *N. luetkeana*, which live along the Pacific coast of North America from Alaska to central California, provide the habitat for a rich community of other organisms (Shaffer 2000; Schoch and Chenelot 2004). The large sporophyte of *N. luetkeana* has about 30–60 blades, which can be up to ~4 m long, attached to a gas-filled “pneumatocyst” (float) that holds them near the surface of the water; a long, slender stipe tethers the pneumatocyst to the holdfast, which is attached to the substratum (Abbott and Hollenberg 1976). The morphometrics, structural mechanics, and hydrodynamics of *N. luetkeana* are described by Koehl and Wainwright (1977), Koehl and Alberte (1988), and Johnson and Koehl (1994), and are modeled by Denny et al. (1997). These kelp form large beds near the shore in water depths of about 3–17 m (Abbott and

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Table 1 Blade shapes in different water flow habitats

Species	Wide in slow flow; narrow in rapid flow	Thin in slow flow; thick in rapid flow	Undulate in slow flow; flat in rapid flow	Heavily corrugated or bullate in slow flow; less so in rapid flow
<i>Agarum fimbriatum</i>		Duggins et al. (2003)		
<i>Costaria costata</i>		Duggins et al. (2003)		
<i>Dictyota</i> sp.	Stewart and Carpenter (2003)			
<i>Durvillaea potatorum</i>	Cheshire and Hallam (1989)	Cheshire and Hallam (1989)		
<i>Ecklonia radiata</i>	Fowler-Walker et al. (2006), Wenberg and Thomsen (2005), Wing et al. (2007)	Wenberg and Thomsen (2005), Wing et al. (2007)	Wing et al. (2007)	
<i>Eisenia arborea</i>	Roberson and Coyer (2004)	Roberson and Coyer (2004)		Roberson and Coyer (2004)
<i>Fucus vesiculosus</i>	Back (1993)			
<i>Gigartina radula</i>	Jackelman and Bolton (1990)	Jackelman and Bolton (1990)		
<i>Hedophyllum sessile</i>	Armstrong (1989)		Armstrong (1989)	Armstrong (1989)
<i>Laminaria complanata</i>		Duggins et al. (2003)		
<i>Laminaria digitata</i>	Sundene (1961)	Sundene (1961)		
<i>Laminaria hyperborean</i>	Sjøtun and Fredriksen (1995)	Sjøtun and Fredriksen (1995)		
<i>Laminaria japonica</i>	Kawamata (2001)		Kawamata (2001)	
<i>Laminaria longicuris</i>	Gerard and Mann (1979)	Gerard and Mann (1979)	Gerard and Mann (1979)	
<i>Laminaria saccharina</i>	Parke (1948)	Parke (1948)	Buck and Buchholz (2005)	
<i>Macrocystis integrifolia</i>	Hurd et al. (1996)	Hurd et al. (1996)	Hurd et al. (1996), Hurd et al. (1997)	Hurd et al. (1996)
<i>Nereocystis luetkeana</i>	Johnson and Koehl (1994), Koehl and Alberte (1988)		Johnson and Koehl (1994), Koehl and Alberte (1988)	
<i>Pachydictyon coraceum</i>	Haring and Carpenter (2007)	Haring and Carpenter (2007)		
<i>Saccorhiza polyschides</i>	Norton (1969)			

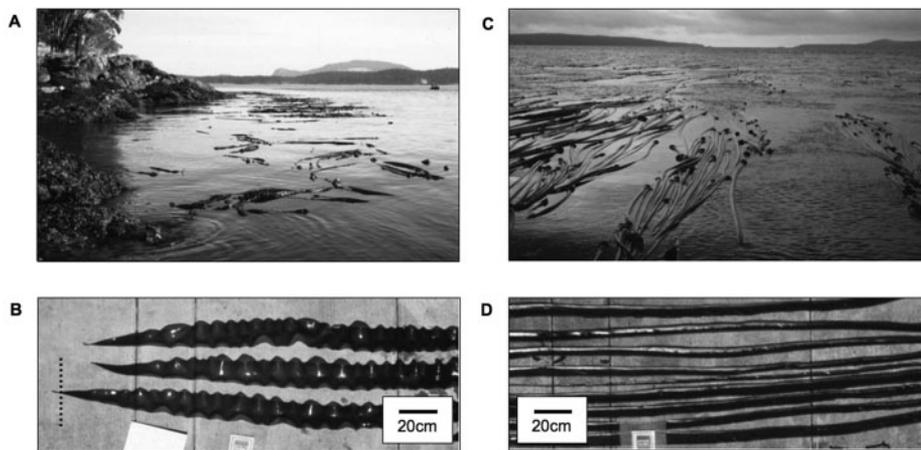


Fig. 1 (A) *Nereocystis luetkeana* bed at SC, the slow-flow habitat. (B) Ruffled, wide blades from a *N. luetkeana* collected at SC. The dotted line indicates the blade position defined as the “origin” in growth experiments (the position along a blade where the blade first widens from a cylindrical string into a flat blade). (C) *Nereocystis luetkeana* bed at TR, the current-swept habitat. (D) Flat, narrow blades from a *N. luetkeana* collected from TR.

Hollenberg 1976) where they are exposed to tidal currents and to nonbreaking waves at some sites (Koehl and Wainwright 1977; Koehl and Alberte 1988; Johnson and Koehl 1994; Gaylord et al. 2003).

The blades of *N. luetkeana* from sites exposed to slow flow are wide and “undulate” (ruffled) (Fig. 1A and B), whereas the blades of those from sites exposed to rapid currents are flat, narrow, and strap-like

(Fig. 1C and D) (Koehl and Alberte 1988; Johnson and Koehl 1994).

The life history of *N. luetkeana* is reviewed by Johnson and Koehl (1994) and Koehl (1999). The sporophytes start growing in the early spring and become tall enough to reach the surface of the water by summer. Their blades grow rapidly as new tissue is added near the proximal end, pushing older tissue distally. The sporophytes generally become reproductive by mid-summer, with spore-producing patches (sori) forming in the older, distal areas of the blades. Sori fall out and older tissue erodes at the distal ends of the blades. Growth rate of the blade slows in the autumn, photosynthetic rate decreases, and the strength of the stipe declines. Most *N. luetkeana* sporophytes are washed away during winter storms, so this species is essentially an annual kelp.

Nereocystis luetkeana are ideal for studying how organisms grow into shapes that correlate with hydrodynamic habitat, not only because the shapes of their blades vary so strikingly between flow regimes, but also because they grow very rapidly. To explore the consequences and causes of the different blade shapes of *N. luetkeana*, we have begun by focusing on four questions:

- (1) What are the differences between the blade morphology of kelp from exposed versus protected sites?
- (2) How does blade morphology affect performance of the kelp in moving water?
- (3) What are the patterns of growth that produce ruffled blades versus flat blades?
- (4) Does shape of the blade change in response to flow environment?

In this article, we briefly review our published results for the first two questions and then present our new work addressing the last two.

Morphological differences between blades in different habitats

Blades of *N. luetkeana* in habitats protected from rapid water flow (Fig. 1B) are wider than those at current-swept sites (Fig. 1D) (Koehl and Alberte 1988; Johnson and Koehl 1994). Although the blades from both flow habitats are very narrow near their proximal attachments to the pneumatocyst, the blades from protected sites are significantly wider than are those from exposed sites at distances of 30 cm or more from the origin (we define “origin” operationally as the position along a blade where the

blade first widens from a cylindrical string into a flat blade; Fig. 1B). Mean blade widths for *N. luetkeana* from the “protected site” used for the growth experiments reported in this study [Shady Cove (SC), peak velocities during flooding tide ~ 0.5 m/s] were about 8–9 cm, whereas those from the “current swept” site we used [Turn Rock (TR), peak velocities during flooding tide ~ 1.5 m/s] were only ~ 4 cm wide (Koehl and Alberte 1988; Johnson and Koehl 1994).

We quantified the degree of undulation of kelp blades using a “ruffle index” (RI), the ratio of the total area of a blade to its projected area (technique described by Koehl and Alberte 1988). Flat blades have a RI of one, while ruffled blades have higher RI's. We found that blades of *N. luetkeana* growing in slow flow were significantly more ruffled (RI ~ 1.1) than were those from current-swept habitats (RI ~ 1) (Koehl and Alberte 1988).

Effects of blade morphology on kelp performance

We studied how blade shape affects the passive motion and reconfiguration of *N. luetkeana* in flowing water, and how that hydrodynamic behavior in turn affects two ecologically important aspects of kelp performance: photosynthesis and susceptibility to breakage.

Motion of blades in moving water

In still water the blades of *N. luetkeana* hang down from the floating pneumatocyst, but in flowing water the blades stream out parallel to the direction of the current, flutter like flags in the wind, and clump together.

Measurements of the up–down motion of individual blades in a flume showed that undulate blades flutter more erratically than do flat blades (Koehl and Alberte 1988). In a flume study, ruffled blades taken from habitats with slowly flowing water flapped up and down at amplitudes of about 2–16 cm, depending on the velocity of flow, whereas strap-like blades from current-swept locations flapped at amplitudes of only ~ 1 –2 cm. The variability of flapping amplitude was also much greater for ruffled blades than for flat ones. Furthermore, flapping amplitude of undulate blades was greatest at current velocities of 0.3–0.4 m/s (typical speeds of tidal currents in their habitats), whereas fluttering amplitude did not change significantly with velocity for strap-like blades at current speeds > 0.2 m/s. Although strap-like blades flutter at lower amplitude,

they move up and down at higher frequency than do ruffled blades.

When subjected to a water current, the many blades on a *N. luetkeana* are pushed together into a clump. We measured the maximum widths of the clumps of blades on kelp as they were towed at defined velocities under an observation bridge (Koehl and Alberte 1988). Dividing width of the clump by the total width of all the blades on that kelp when laid out side-by-side yields a “clump index” (CI), which provides a measure of how spread out the blades on that kelp are in moving water. For both blade morphologies, CI decreased as velocity increased. However, the strap-like blades of kelp from current-swept sites collapsed together into narrow, streamlined bundles with CI's about half that of the wide, ruffled blades of kelp from habitats with slow flow. To test the role of ruffles versus blade width in clumping behavior, the ruffled blades of protected-site kelp were replaced with flat plastic replicas of those blades and the towing experiments were repeated. Such flat, wide models had CI values intermediate between the CI's of ruffled, wide blades and those of flat narrow blades, indicating that both the width and the ruffling of blades affect clumping.

Photosynthesis

When the blades of a *N. luetkeana* are pushed into a clump by flowing water, the blades within the clump are shaded by the blades above them (Koehl and Alberte 1988). Field measurements showed that when the strap-like blades of a *N. luetkeana* at an exposed site collapsed into a streamlined bundle and fluttered at low amplitude, the flux of photosynthetically active radiation (PAR) reaching blades within the clump was reduced by about 70% compared with the PAR flux encountered by the blade at the top of the bundle. During the early morning and late afternoon, especially in the cloudy weather that commonly occurs where *N. luetkeana* grows, such self-shading can reduce the photosynthetic rates of the blades within the clump. In contrast, field measurements of light under the ruffled blades of *N. luetkeana* at a protected site showed that the PAR flux to the lower blades in a clump was reduced by only about 16% as the undulate blades flapped erratically and remained spread out in flowing water. Thus, *N. luetkeana* illustrate that a ruffled blade shape can reduce self-shading for macroalgae with multiple blades in flowing water.

We measured uptake rates of bicarbonate (an important source of carbon for algal photosynthesis) by blade tissue of *N. luetkeana* in a flume at slow

water velocities (<0.9 m/s) at which mass exchange at blade surfaces limited photosynthesis (Koehl and Alberte 1988). We found that blade flapping stirred the water near blade surfaces and enhanced rates of uptake, and thus of photosynthesis, when ambient currents were slow. Undulate blades flap at greater amplitude, but lower frequency, than do strap-like blades; hence their up-down speeds through the water are similar. To test whether shape of the blade affects the rate of mass exchange, we conducted field experiments in which time-averaged rates of mass exchange at the surfaces of blades were measured by the loss of weight of dissolving candy life savers sewn to blades (Koehl and Alberte 1988). We found that there was no difference between the rates of mass exchange of ruffled and strap-like blades on *N. luetkeana* transplanted to side-by-side positions exposed to the same slack-tide flow conditions under which uptake is likely to limit photosynthesis.

Susceptibility to breakage

A major cause of mortality for *N. luetkeana* is being washed away by ambient water flow (Koehl and Wainwright 1977; Duggins et al. 2001). The hydrodynamic drag per area of blade measured for intact *N. luetkeana* towed at a range of velocities up to 2.0 m/s was greater for individuals with wide, ruffled blades than for those with narrow, flat blades (Koehl and Alberte 1988). To measure the contribution to drag of ruffles versus blade width, we replaced the ruffled blades of kelp from protected sites with flat plastic replicas of those blades and repeated the measurements of drag. Such flat, wide models had values of drag per area of blade that were intermediate between those of ruffled, wide blades and those of flat narrow blades. Thus, both the width and the extent of ruffling of blade edges affect drag.

Environmental stress factor (ESF) is the ratio of the strength of an alga (force per area to break its stipe or holdfast) to the stress (force per area) in those structures due to the hydrodynamic forces on the organism at a particular stage in its life (i.e., at a defined age, habitat, and season). The lower the ESF, the greater the chance that an organism will be swept away by ambient currents. We found that the ESF's (calculated using stipe strength) of *N. luetkeana* from protected and current-swept sites were not significantly different from each other (ESF's of ~ 6 – 12 during the summer) (Johnson and Koehl 1994). Even though the drag per blade area was greater on ruffled blades, total blade area per individual was smaller, peak water velocities encountered were lower, and strength of the stipe was higher at the protected site.

However, in the autumn and winter, as growth and reproductive output of *N. luetkeana* slows, strength of the stipe deteriorates as damage accumulates, and the frequency of storms increases, ESF's decrease and the kelp are swept away (Johnson and Koehl 1994). When storms hit, Duggins et al. (2001) found that mortality was higher for *N. luetkeana* that had been growing in calm water than for those that had developed at sites with fast flow. While our study focused on *N. luetkeana* exposed to tidal currents, other populations are exposed to waves. Although the hydrodynamic performance and probability of breaking of *N. luetkeana* with strap-like blades exposed to waves has been studied (Denny et al. 1997), a comparable analysis of kelp with wide, ruffled blades has not yet been carried out.

Patterns of blade growth that produce ruffles versus straps

We measured the spatial patterns of growth of blades on *N. luetkeana* living at a protected site (SC, Fig. 1A) and at a current-swept site (TR, Fig. 1C) to determine how ruffled blades versus flat blades are produced. At each site, the pneumatocyst and blades of haphazardly selected kelp were pulled onto the deck of a boat anchored at the edge of the kelp bed. One undamaged blade of each plant was spread on a marked grid that served as a template for a series of holes that were punched into the blade by a hollow brass rod 2 mm in diameter (Fig. 2A, upper photograph). The distances between the distal edges of the holes in rows along the length of the blade were determined to the nearest millimeter using a flexible tape measure (Fig. 2B). We used the flexible tape because distances measured with a rigid ruler or by

digitizing photographs of blades would have underestimated the lengths between holes in ruffled regions of blades. Transverse distances between the left edges of holes in adjacent rows were also measured to the nearest millimeter (Fig. 2C). These kelp were left to grow *in situ* for 6 days, the marked blades were collected, and the distances between holes were measured again (Fig. 2A, lower photograph). We measured growth during June when blades grow rapidly (Johnson and Koehl 1994).

We used "strain rate" as a rough measure of local growth rate within a blade. The increase in length (ΔL) of the distance between adjacent holes in a row during the experiment represents the new longitudinal growth of the tissue between those holes (Fig. 2B). We normalized that new growth to the length of the tissue segment by dividing ΔL by the original distance between the holes (L_0) at the start of the experiment ($\Delta L/L_0 = \text{longitudinal strain}$). Transverse strains ($\Delta W/W_0$, where ΔW is the increase in distance between adjacent rows of holes, and W_0 is the original distance between them; Fig. 2C) were determined in a similar manner. We calculated rough estimates of local strain rates within blades by dividing the local strain of each marked segment of a blade by the number of days that segment was growing during the experiment.

Longitudinal strain rates for undulate blades growing at the protected site are shown in Fig. 3A and those for strap-like blades growing at the exposed site are presented in Fig. 3B. Strain rates are plotted as a function of the distance from the origin (see dotted line in Fig. 1B), where distance is assigned to the position of the proximal hole marking a segment of the blade at the start of the experiment. These plots show that some parts of the

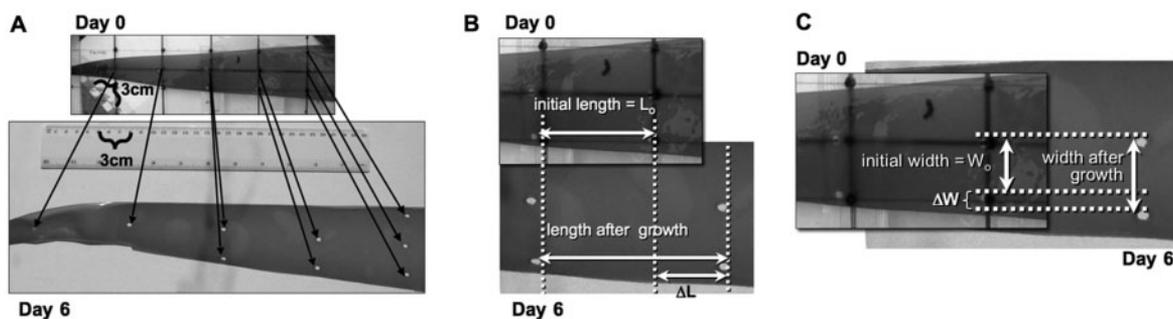


Fig. 2 (A) A grid of holes was punched in a blade on Day 0 of a growth experiment (upper photograph) and the distances between the holes were measured. On Day 6 (lower photograph) the distances between those holes were measured again. (B) Longitudinal growth (ΔL) was calculated by subtracting the initial length (L_0) between the distal edges of two adjacent holes along a row parallel to the long axis of the blade, from the distance between the distal edges of those holes ("length after growth") on Day 6. (C) Transverse growth (ΔW) was calculated by subtracting the initial width (W_0) between the left edges (when the blade was viewed from the pneumatocyst) of two adjacent holes along a column perpendicular to the long axis of the blade, from the distance between the left edges of those holes ("width after growth") on Day 6.

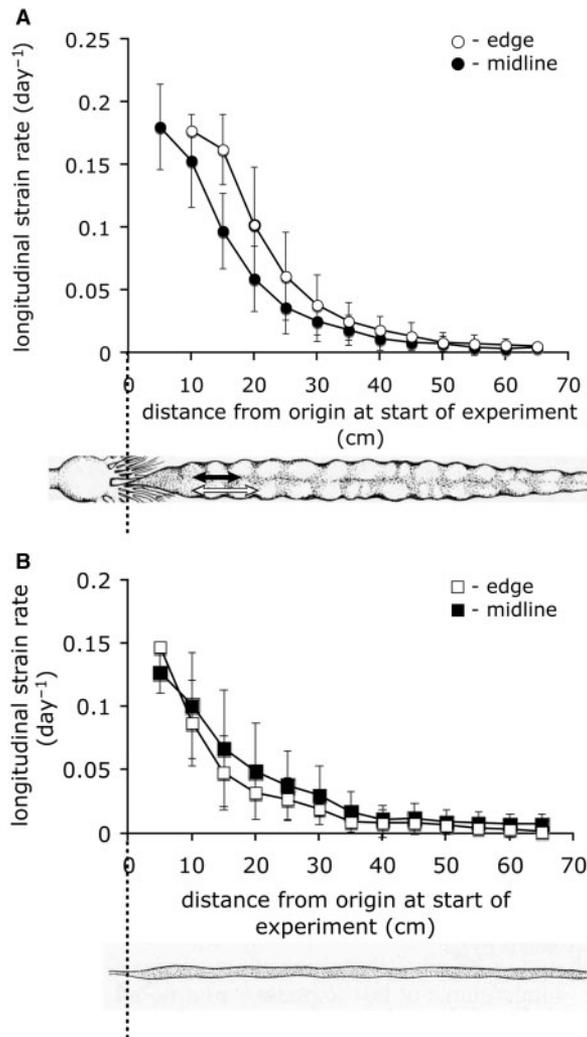


Fig. 3 Longitudinal growth strain rates ($[\Delta L/L_0]/\text{day}$) plotted as a function of the distance from the origin (Fig. 1C) of the proximal hole marking a blade segment at the start of the experiment on Day 0 for ruffled blades on *N. luetkeana* ($n=9$ kelp) growing at the slow-flow SC site (A), and for strap-like flat blades on *N. luetkeana* ($n=5$ kelp) growing at the current-swept TR site (B). Open symbols indicate longitudinal strain rates measured along the edge of a blade, as indicated by the white arrow on the blade diagram in (A). Black symbols indicate longitudinal strain rates measured along the midline of a blade, as illustrated by the black arrow on the blade diagram in (A). Error bars show 1 SD. Longitudinal strain rates at the proximal ends of ruffled blades (starting positions 10 and 15 cm from the origin) were significantly greater along the blade edges than along their midlines (ANOVA, $P<0.05$), whereas there was no significant difference between edge and midline strain rates for the flat blades.

blades grow more rapidly than others (Figs 3, 4, and 7). During the course of an experiment, the segments of the blade move continuously away from the origin, thus more analysis is needed to show the total growth of a tissue element over time. Our analysis of the trajectories of tissue growth and of

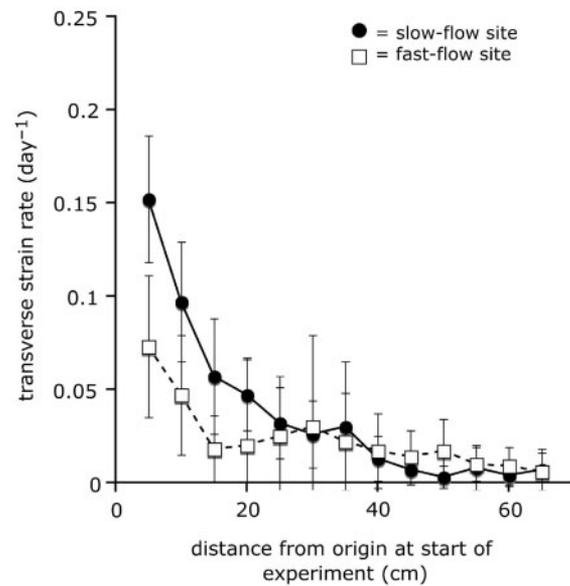


Fig. 4 Transverse growth strain rates ($[\Delta W/W_0]/\text{day}$) plotted as a function of the distance from the origin (Fig. 1C) of each transverse column of holes at the start of the experiment on Day 0, for wide, ruffled blades on *N. luetkeana* growing at the slowflow SC site (black circles, $n=9$ kelp), and for narrow, flat blades on *N. luetkeana* growing at the current-swept TR site (open squares, $n=5$ kelp). Error bars represent 1 SD. Transverse strain rates for the wide, ruffled blades were significantly greater than those for narrow, flat blades at the proximal ends of the blades (starting positions of 5, 10, and 15 cm from the origin) (ANOVA, $P<0.05$).

growth strains as a function of position will be presented elsewhere.

Longitudinal strain rates of both undulate (Fig. 3A) and flat (Fig. 3B) blades are greatest near the blade's origin, but continued growth of older tissues at distances of 30–50 cm from the origin is evident. In the rapidly growing proximal regions of ruffled blades, the edges of the blade grew more rapidly than did the midlines (Fig. 3A). In contrast, the longitudinal strain rates of the edges and midlines of flat blades did not differ from each other (Fig. 3B).

Transverse strain rates of both ruffled and flat blades are plotted in Fig. 4. As with longitudinal growth, most growth in width occurs at the proximal ends of the blades. Ruffled blades growing at the site with slow flow had higher rates of transverse strain than did flat blades growing at the exposed site.

In addition to length and width, we also measured blade thickness to the nearest 0.1 mm with vernier calipers. Blades of both morphologies were thicker at their proximal ends than they were distally. At a position 5 cm from the origin, the mean thickness of ruffled blades was 0.9 mm (SD = 0.15, $n=12$ kelp) and the mean thickness of strap-like blades was

1.0 mm (SD = 0.19, $n = 5$ kelp); these proximal thicknesses were not significantly different from each other (ANOVA, $P = 0.25$). In contrast, at more distal positions, ruffled blades from the protected habitat were thinner than flat blades from the current-swept site. For example, at a position 60 cm from the origin, the thickness of ruffled blades (mean = 0.5 mm, SD = 0.07, $n = 12$ kelp) was significantly lower than that of strap-like blades (mean = 0.7 mm, SD = 0.11, $n = 5$ kelp) (ANOVA, $P = 0.009$). Such small differences in the thickness of a blade can have a large effect on its bending energy, and hence on the tendency of the blade to form ruffles by elastic buckling.

Ruffles form by elastic buckling

Observations reveal a new twist

When *N. luetkeana* blades grow in habitats exposed to rapid water currents, their edges and midlines elongate at the same rate (Figs 3B and 7), whereas when they grow at sites protected from rapid flow, their edges elongate at a greater rate than their midlines (Fig. 3A). We hypothesize that the ruffles along the edges of blades at protected sites are formed by elastic buckling when a gradient in growth rates exists between the midline and the edges of a blade.

A number of observations indicate that the ruffles on *N. luetkeana* blades form by elastic buckling of the edges of blades that have grown longer than the midline. The wavelengths and amplitudes of ruffles are not fixed, but rather can easily be changed by pushing on different points along a blade's edge. When pushed, the edge of an undulate blade can suddenly pop into a different configuration of ruffles, as illustrated by Fig. 5A, which shows various patterns of ruffles taken on by the same section of a blade's edge. Such popping between different configurations when pushed is typical behavior for elastically buckled structures (Timoshenko and Gere 1961). The wavelengths of ruffles that we produced by pushing on live blades corresponded to a pattern we had noticed when measuring ruffles on photographs of blades: some ruffles had wavelengths half as long or twice as long as the most frequently observed wavelength (Fig. 1B). Blades that are ruffled when lying on a flat surface can become twisted ribbons when hanging without constraint (Fig. 5B) or when drifting in the water. When a blade is free to twist, the wavelengths of the ruffles along its edges tend to be greater than when the blade lies on a surface. Furthermore, a blade can easily snap between being a right- or a left-handed helix (Fig. 5C).

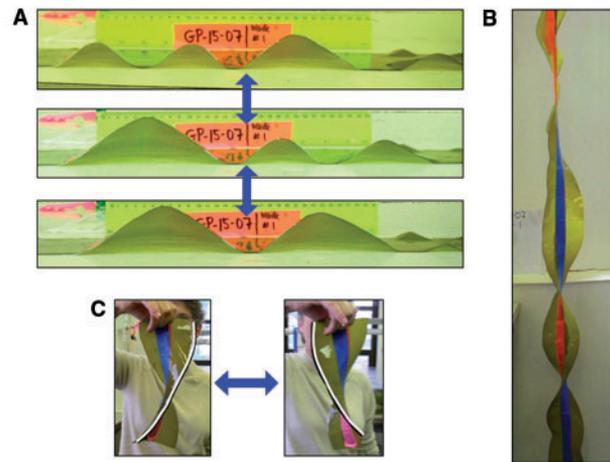


Fig. 5 (A) Photographs of the edge of a ruffled *N. luetkeana* blade on a table. Pushing on the edge of the blade caused it to snap between different ruffle configurations, three of which are shown in these photographs. Numbers on the ruler are 1 cm apart. (B) A ruffled *N. luetkeana* blade hanging in air twisted into a helicoidal configuration. A strip of blue flagging tape was laid along one surface of the blade and a strip of orange tape along the opposite surface so that the twists in the blade would be easier to see. (C) A section of a ruffled *N. luetkeana* blade was easily flipped back and forth between right- and left-handed twists. A strip of blue flagging tape marked one surface of the blade and a strip of pink tape marked the opposite side. A white line has been drawn on the edge of the blade to make the twist easier to see.

A model for ruffle formation by elastic buckling

Mathematical models of the buckling of thin elastic plates due to the influence of mechanical loads can provide insights into the physical mechanisms involved in morphogenetic processes such as the emergence of the primordium of plant organs (Green 1992; Green et al. 1996), wrinkling of sheets (Cerdeña and Mahadevan 2003), and multiscale ruffling of leaves and flower petals (Sharon et al. 2002, 2004, 2007). Although the complex geometries explored by these various models differ, the basic underlying mechanism is the same. If some parts of the sheet grow more than others, material points in the sheet move relative to each other, which leads to “growth strains” (Erickson 1966; Silk 1984). If these strains are not homogeneous, the material of the sheet is subjected to mechanical stresses as different parts of it pull and push on each other (e.g., if some parts of the sheet increase in area more than others, the faster-growing areas are under in-plane compression and the slower growing areas are under in-plane tension). If these stresses that act in the plane of the sheet are large enough, the sheet responds by buckling and bending out of the plane, thereby causing ruffles to develop. The wavelengths, amplitudes, and positions of the ruffles, wrinkles, bumps,

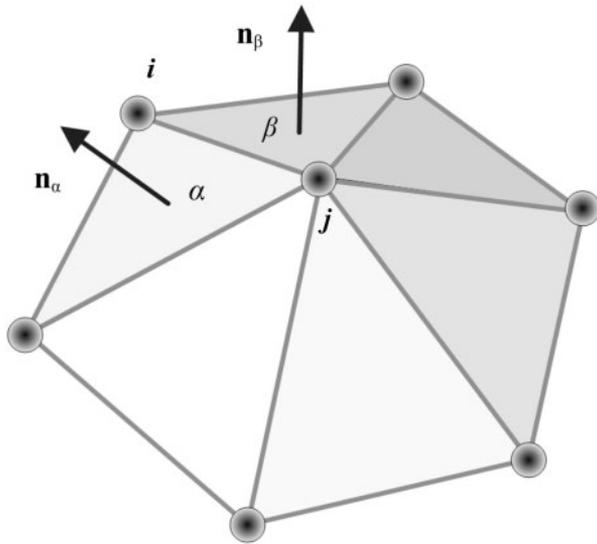


Fig. 6 The blade is modeled as a triangular mesh of springs that resist stretching and bending deformations with the energy given in Equation (1). Symbols are defined in the text.

and twists that occur in specific cases depend on the mechanical properties and dimensions of the plate, and on the spatial distribution of differential growth strains.

To understand the development of flat blades in exposed habitats and ruffled blades in protected habitats, it is useful to consider the slow growth of a long, thin, lamina. We assume that there are no variations in the growth rate across the thickness of the lamina (i.e., that one surface of the blade does not grow faster than the other). If all elements of the blade grow at the same rate in length and width, the blade increases in size, but does not change its shape, while if elements in the blade grow uniformly in length, but do not grow in width, the blade elongates without changing its width. However, in the presence of differential growth, so that some parts of the blade grow more than others, thus straining the tissue, the blade could ruffle.

In the simplest case, we model the algal blade as a thin elastic sheet of length L , width W , and thickness h (where $h \ll W \ll L$) that is naturally flat in the absence of any external forces. In our computational model, we treat the blade as a triangulated spring network (Fig. 6) with the energy U required to stretch and bend it that may be written as

$$U = \sum_{i,j} \frac{3Y}{4} (|\mathbf{r}_i - \mathbf{r}_j| - l_{ij})^2 + \sum_{\alpha,\beta} \frac{2B}{\sqrt{3}} (1 - \mathbf{n}_\alpha \cdot \mathbf{n}_\beta) \quad (1)$$

(Seung and Nelson 1988). The first term in Equation (1) is the “stretching energy,” which is the pair-wise sum, over all nodes i and j , of the energy required to

change the length of a spring in the network. The spring has a natural length l_{ij} that connects two nodes in the network with position vectors \mathbf{r}_i and \mathbf{r}_j . Y is the 2D Young’s modulus (i.e., resistance to being pulled or compressed) of the spring. The second term in Equation (1) is the “bending energy,” which is the pair-wise sum, over all triangle pairs α and β , of the energy required to bend the network, and thus to change the dihedral angle between adjacent triangles with normals \mathbf{n}_α and \mathbf{n}_β (Fig. 6). The bending stiffness, B , is the resistance of that angle to being changed. Since relative growth changes the natural distance between material points, we can simulate such growth in our model of an elastic sheet by making the natural length (l_{ij}) of the springs in our network be a function of their position in the sheet. We can also modify this basic template to account for inhomogeneity in the stiffness of the blade by allowing Y and B to depend on position in the blade. Similarly, we can model anisotropy in tissue stiffness by making Y and B depend on direction.

We simulate a higher growth rate along the edges than the midline of a blade consistent with our measurements (Fig. 3A) by making the natural length (l_{ij}) of the springs an increasing function of lateral distance from the midline (we describe this function using a simple polynomial form). We then relax the strain energy in the blade [given by Equation (1)] using a damped molecular dynamics simulation (details described in Allen and Tildesley 1987) until the blade eventually reaches equilibrium in the presence of the internal strains induced by the differential growth. In Fig. 7 we show examples of the resulting ruffled and twisted blades that arise if: (1) one edge of the blade grows more than the other (Fig. 7A), or (2) both edges of the blade grow more than the midline, the edges have the same growth rate as each other, and the bending stiffness of the blade in the transverse direction is larger than the bending stiffness in the longitudinal direction (Fig. 7B). Further work remains to be done to apply this analysis to measured geometries, tissue stiffnesses, and gradients in growth rates in blades of *N. luetkeana* to determine whether the ruffling geometries predicted by this elastic growth model match those observed for real kelp blades.

Shape of the blade changes in response to flow

Reciprocal transplant experiments

We conducted a series of reciprocal transplant experiments during June to determine whether *N. luetkeana*

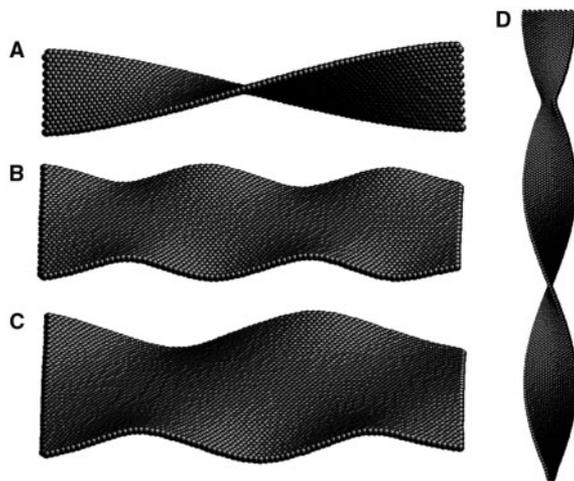


Fig. 7 Numerical simulations demonstrate different buckling morphologies of growing kelp blades. For all three cases, the length is assumed to be the same (80 units) with widths of 20, 40, and 60 units. We see that there is a qualitative transition from global buckling to localized edge buckling as the aspect ratio of the blade is changed. For the same inhomogeneous growth profile, narrow blades respond by twisting globally into helicoidal shapes (A) while broad blades respond by undulating only in the vicinity of the lateral edges (B, C). It is easy to understand this transition qualitatively: when the blade width $w \gg \lambda$ (edge wave length), the bulk of the kelp remains flat while the edges buckle to accommodate the growth, while when $w/\lambda \sim 1$, the coupling between the edges causes a transition from local buckling to global twist. Indeed, sometimes it is possible for both localized edge buckles and global twist modes to coexist, as can be seen in (D). For all simulations, the parameters chosen were such that the ratio of the bending stiffness B to the stretching stiffness Y is approximately $1/50$ (only the ratio appears in the scaled energy).

can change the morphology of their blades in response ambient water flow. Kelp with wide, ruffled blades collected from the protected SC site were tied to cinder blocks that held them in place when they were transplanted into the current-swept TR site. Kelp with narrow, flat blades collected at TR were transplanted into the SC site in the same way. All transplanted kelp were placed at depths where their pneumatocysts could float at the air–water interface. Grids of holes were punched into one undamaged blade per kelp, as described above (Fig. 2A) and the distances between holes were measured before the kelp were transplanted, and again after 6 days of growth in their new flow environments (Fig. 2B and C). Marked blades of kelp growing *in situ* at SC and TR during the same 6-day period served as controls (Figs 3 and 4).

We found that the new proximal regions of blades changed their morphology when *N. luetkeana* were transplanted to different flow regimes. For example, the proximal sections of ruffled blades from the

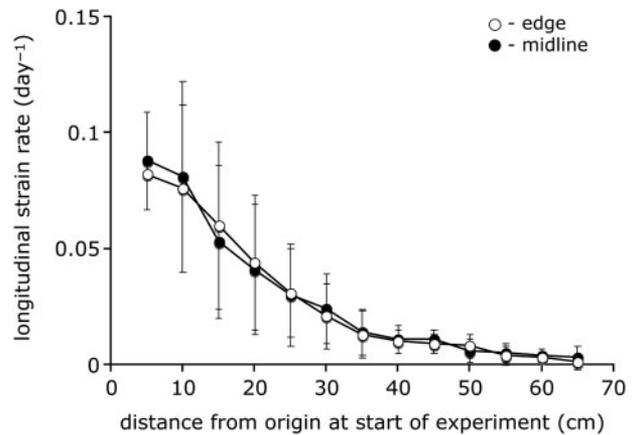


Fig. 8 Longitudinal growth strain rates ($[\Delta L/L_0]/\text{day}$) plotted as a function of the distance from the origin (Fig. 1C) of the proximal hole marking a blade segment at the start of the experiment on Day 0 for ruffled blades on *N. luetkeana* transplanted from the protected SC site to the current-swept TR site ($n = 6$ kelp). Open circles indicate longitudinal strain rates measured along the edge of a blade, and black symbols indicate longitudinal strain rates measured along the midline of a blade. Error bars show 1 SD. There were no significant differences between edge and midline strain rates for blades on these transplanted kelp (ANOVA, $P > 0.05$).

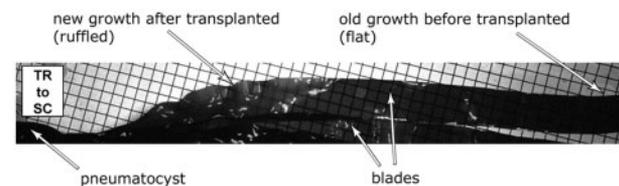


Fig. 9 Photograph (taken 6 days after the transplant) of the proximal end of some blades of a *N. luetkeana* transplanted from the current-swept TR site to the slowflow SC site (grid marks 1 cm apart). The old, slowly growing distal portion of the blade retained the flat blade morphology that characterized this individual before it was transplanted, while the new, rapidly growing proximal portion of the blade developed ruffles. All individuals ($n = 5$ kelp) transplanted from the current-swept to the slow-flow habitat showed similar development of ruffles in the new proximal blade tissue. In contrast, the blades of all control kelp ($n = 5$) collected from the current-swept site and transplanted back into that exposed site remained flat.

slow-flow site became flat after being transplanted to the current-swept site. This flat shape was produced because the longitudinal strain rates along the edges of the blades of such transplanted kelp were the same as those along the midlines of the blades (Fig. 8). Conversely, the new tissue at the proximal ends of strap-like blades on kelp transplanted from the current-swept to the slow-flow site were ruffled (Fig. 9).

Although we observed changes in the shapes of blades of *N. luetkeana* transplanted to different flow

environments, we did not see the morphologies of our transplanted kelp fully converge with those of the individuals living at that site. Our experiments lasted only 6 days, whereas common garden experiments with *Macrocystis integrifolia* showed that transplanted kelp continued to change in form over periods of many months before their morphologies converged (Druehl and Kemp 1982).

Mechanical load affects shape of the blade

One proximate cue of flow that might affect the growth of kelp blades is the mechanical load on a blade due to hydrodynamic force. We tested this idea by conducting a series of growth experiments in which blades of *N. luetkeana* were pulled by weights that simulated the magnitude of the drag that a blade of that shape would experience during peak tidal currents at the protected SC cite or at the current-swept TR site. These experiments were conducted using intact kelp suspended in large, clear outdoor tanks (Fig. 10A) exposed to ambient sunlight. Running seawater circulated through the tanks (input flow rate of ~ 0.13 l/s), keeping the kelp bathed in well-aerated seawater at ambient ocean temperature ($9\text{--}11^\circ\text{C}$) without exposing them to a directional water current. Six individuals (three from the current-swept site and three from the slow-flow site) were hung in each tank and the support rack was rotated daily so that each individual was in a different position for each of the 6 days of an experiment.

The experimental treatments of blades are illustrated in Fig. 9B. Grids of holes (described above, Fig. 2) were punched into three undamaged blades on each experimental kelp. A weight that simulated the drag on a blade in a water current of 0.5 m/s (similar to the peak tidal currents at the slow-flow SC site) was hung on one marked blade, a weight simulating drag on a blade in a water current of 1.5 m/s (similar to the peak tidal currents at the fast-flow TR site) was hung on another marked blade, and the third marked blade was not subjected to any added weight. Drag on the blades of individuals collected from TR and from SC were calculated using the mean drag per unit area of blade we measured at 0.5 m/s and at 1.5 m/s on *N. luetkeana* from TR with strap-like blades, or from SC with ruffled blades, respectively (Koehl and Alberte 1988). The end of each experimental blade was protected by plastic screen and was folded over and stitched together to make a loop; a weight equivalent to the simulated drag was hung from twine threaded through that loop to evenly distribute the load across the width of the blade. Three replicate experiments were

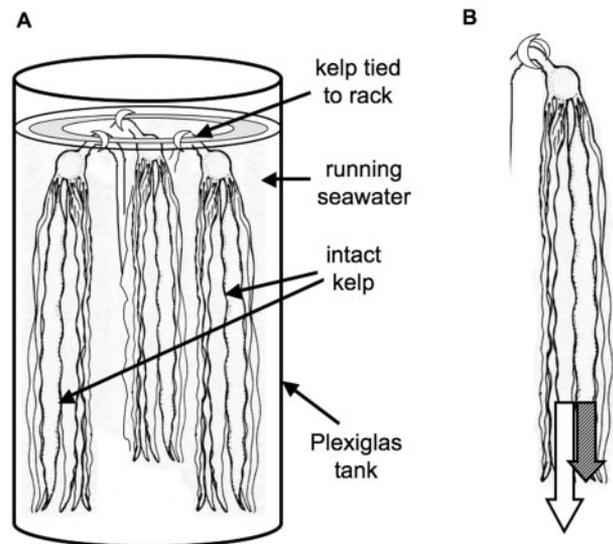


Fig. 10 (A) Diagram of *N. luetkeana* suspended in a clear Plexiglas tank (diameter = 1 m, depth = 2 m) for laboratory growth experiments. Two such tanks, standing outside side-by-side exposed to ambient sunlight, were used for the experiments. Six individuals (three from the current-swept site and three from the slow-flow site) were hung in each tank (only three are diagrammed here for simplicity). (B) Diagram of the mechanical treatments tested in our tank growth experiments. For each individual, the growth of three blades was monitored. One blade was subjected to a weight (indicated by the hatched arrow) equivalent to the drag force that one blade of the same shape (i.e., wide and ruffled, or narrow and flat) would experience in a water current of 0.5 m/s (similar to the peak tidal currents at the slow-flow SC site). A second blade was subjected to a weight (indicated by the white arrow) equivalent to the drag force that one blade of the same shape would experience in a water current of 1.5 m/s (similar to the peak tidal currents at the fast-flow TR site). A third blade was subjected to no additional mechanical load.

conducted in June and July, but some kelp were lost when the seawater pipes to tanks clogged. Growth rates of blades were not significantly different between experiments, so the data were pooled.

Mechanical load affected the shape of the rapidly growing proximal regions of the experimental blades, as illustrated in Fig. 10. The new proximal regions of the blades that had been exposed to forces simulating the drag they would experience in a water current of 1.5 m/s were flatter and narrower than were the new proximal sections of blades exposed to no external load or to forces mimicking the drag they would experience in a current of 0.5 m/s. We observed this pattern both for blades that were wide and ruffled at the start of the experiment (Fig. 11A), and for blades that were initially narrow and flat (Fig. 11B), although the effect was more striking for the ruffled

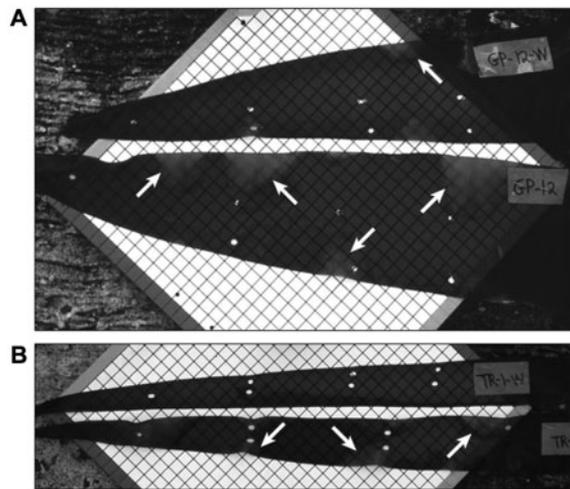


Fig. 11 Photographs of blades of *N. luetkeana* after 6 days of growth in the tank experiments illustrated in Fig. 9. White arrows indicate the positions of ruffles. The initial length (L_0 , see Fig. 2B) between the holes punched in the blades at the start of the experiment was 5 cm on Day 0. Lines on the grids are 1 cm apart. **(A)** Blades of an individual collected from the slow-flow site that were initially wide and ruffled. The new growth on the upper blade, which had been subjected to a weight that simulated drag on a ruffled blade exposed to a current of 1.5 m/s, was relatively flat and was narrower than the new ruffled region of the lower blade on which no weight had been hung. **(B)** Blades of an individual collected from the current-swept site that were initially narrow and flat. The new growth on the upper blade, which had been subjected to a weight that simulated drag on a strap-like blade exposed to a current of 1.5 m/s, was flat and was narrower than the new ruffled region of the lower blade on which no weight had been hung.

blades from the protected site than for the strap-like blades from the exposed site. As described earlier, blades become ruffled when their edges grow in length at a greater rate than that of their midlines. In the rapidly growing region of initially ruffled blades (starting position 10 cm from the origin), the ratio of the longitudinal strain rate along the edge of the blade to the longitudinal strain rate along the midline was greater for blades on which no weights had been hung (median ratio = 1.05) than on blades subjected to the “drag” at the slow-flow site (median ratio = 1.02) or on blades exposed to the “drag” at the fast-flow site (median ratio = 0.94) (Kruskal-Wallis, $P = 0.0091$, $df = 2$, $n = 11$ kelp).

Discussion

Aspects of morphology of macroalgae that vary between flow environments

We used *N. luetkeana* to study some of the consequences and causes of having narrow, flat blades in habitats exposed to rapidly flowing water versus

having wide, ruffled blades at sites sheltered from fast motion of water. Seaweeds have a variety of other morphological features that vary with flow habitat that merit further study as well.

A number of macroalgal structural features that vary between different flow habitats relate to the resistance of a thallus to being ripped from the substratum. For example, a number of species have larger holdfasts (Norton 1986; Sjøtun and Fredriksen 1995; Duggins et al. 2003; Roberson and Coyer 2004; Wernberg and Thomsen 2005; Stewart 2006a) or wider stipes (Blanchette et al. 2002; Duggins et al. 2003; Kitzes and Denny 2005; Wernberg and Thomsen 2005; Fowler-Walker et al. 2006) when growing at exposed sites than when in protected habitats. The tenacity (force required to dislodge an alga from the substratum) of a number of species is greater at wave-swept or current-swept sites than in sheltered locales (Jackelman and Bolton 1990; Kawamata 2001; Duggins et al. 2003; Thomsen et al. 2004), while other species show no difference in tenacity between flow habitats (D’Amours and Scheibling 2007). The strength of algal tissues (Johnson and Koehl 1994; Duggins et al. 2003; Kitzes and Denny 2005; Stewart 2006a) and of blades (Duggins et al. 2003) can also differ between flow habitats. Similarly, Martone (2006, 2007) found that tissues of the alga, *Calliarthron* sp. become stronger (due to thickening of the cell walls) as a thallus grows and the hydrodynamic forces it experiences become greater.

A variety of other features that vary between members of a species that live in different flow environments are attributes that can affect both hydrodynamic forces on a thallus and the alga’s photosynthetic performance. For example, some species have smaller blades (Bäck 1993; Molloy and Bolton 1996; Blanchette et al. 2002) or smaller thalli (Cheshire and Hallam 1989; Carrington 1990; Jackelman and Bolton 1990; Blanchette 1997; Wernberg and Thomsen 2005; Stewart 2006a) at exposed sites than in sheltered locales. The blades of some species have more spines or papillae (Jackelman and Bolton 1990; Wernberg and Thomsen 2005), or more perforations (Cheshire and Hallam 1989) in protected habitats. Branching algae can be bushier at slow-flow sites (Cheshire and Hallam 1989; Gutierrez and Fernandez 1992; D’Amours and Scheibling 2007) but some species develop shorter branches in high-flow habitats (Haring and Carpenter 2007). Some species that have air bladders in sheltered environments have smaller or no such floats at exposed sites (Dromgoole 1981; Bäck 1993; Stewart 2004, 2006a).

Some species of macroalgae whose morphology varies with flow habitat maintain the same ESF as they grow in different flow environments (*N. luetkeana*: Johnson and Koehl 1994; *Turbinaria ornata*: Stewart 2006a). However, along coasts exposed to seasonally predictable storms, ESF's can differ between sites during the stormy season and can fall below 1, but the selective pressures against such morphologies should be low for species that reproduce before the stormy season arrives (Koehl 1986; 1999; Wolcott 2007), or for which breakage is an important mechanism of dispersal (Stewart 2006b).

Functional consequences of ruffles and wrinkles

The ruffles, wrinkles, and bullations of macroalgal blades have been shown to affect a variety of aspects of performance. We found that ruffled blades of *N. luetkeana* flutter erratically in flowing water, thereby reducing self-shading. Wrinkles and ruffles also can improve interception of light in other ways. Hurd et al. (1997) found that such blades reorient parallel to the flow, and thus normal to incident sunlight, more easily in slowly moving water than do flat blades. Corrugated blades are also more resistant to bending than are flat blades of the same thickness and stiffness, and thus are more likely to resist folding into a compact, self-shading clump in flowing water (Koehl 2000). Another consequence of wrinkled, bullate, and undulate blade surfaces is that they can induce turbulence in the water flowing across them, thereby enhancing uptake of nutrients (Hurd and Stevens 1997; Hurd 2000; Roberson and Coyer 2004).

Ruffles can increase the hydrodynamic drag on blades (Buck and Bucholz 2005), as we found for *N. luetkeana*. However, some studies suggest that thallus shape might not have important consequences on the hydrodynamic forces on macroalgae. Flexible organisms like macroalgae are passively reconfigured into more streamlined shapes with lower drag coefficients as flow velocity increases (Koehl 1977, 1999, 2000; Vogel 1984; Hawes and Smith 1995; Shaughnessy et al. 1996; Blanchette 1997; Kawamata 2001; Blanchette et al. 2002; Harder et al. 2004; Boller and Carrington 2006a, 2007; O'Hare et al. 2007). Carrington (1990) and Haring and Carpenter (2007) found that algae with different shapes converged onto similar drag coefficients when exposed to the high-flow velocities most likely to break them, and Milligan and deWreede (2004) found that the drag on both the protected and the exposed forms of flexible *Hedophyllum sessile* depended on their size, not their shape. Denny (2006) argued that, for such flexible organisms, hydrodynamic forces may not have been an

important selective factor in the evolution of thallus shape. Our drag data for *N. luetkeana* suggest that the aspects of morphology that are important for the hydrodynamic performance of flexible algae are those that affect the ability to reconfigure into a streamlined shape.

Trade-offs between photosynthesis and hydrodynamic performance

Our study of *N. luetkeana* showed that wide, ruffled blades remain spread out and flutter erratically in moving water, thereby enhancing interception of light while also increasing drag and the risk of breakage, whereas strap-like blades collapse into streamlined bundles and flutter at low amplitude in flowing water, thus reducing both drag and interception of light. Similarly, Haring and Carpenter (2007) measured photosynthetic rates of the branching alga, *Pachydictyon coriaceum*, in a flume and found that individuals from wave-exposed habitats that reconfigured into compact, streamlined bundles in flowing water had lower photosynthetic rates than did individuals from protected sites with morphologies that did not streamline as effectively. Stewart and Carpenter (2003) also found that reconfiguration of the thallus of *Dictyota* sp. in flowing water caused self-shading and reduced photosynthesis. A number of other investigators of macroalgal functional morphology have also suggested that there is a trade-off between morphological features that enhance photosynthesis and those that reduce the risk of breakage by hydrodynamic forces (Gerard and Mann 1979; Littler and Littler 1980; Norton et al. 1982; Jackelman and Bolton 1990; Kubler and Dudgeon 1996; others reviewed in Koehl 1986; Haring and Carpenter 2007).

One mechanism of balancing the trade-offs between photosynthetic and hydrodynamic performance is having the ability to adjust morphology in response to environmental conditions.

Morphological plasticity of macroalgae

Our field transplant experiments revealed that shape of the blade in *N. luetkeana* is a plastic trait: the patterns of growth of new blade tissue changed to produce strap-like shapes in the rapid-flow site and ruffled contours in the slow-flow habitat. Several other species of macroalgae have also been shown to alter their morphology in response to flow. For example, the blades of *Laminaria hyperborea* (Svendsen and Kain 1971), *Laminaria longicuris* (Gerard and Mann 1979), and *Laminaria digitata* (Sundene 1961) changed shape when transplanted to different flow regimes in ways akin to the changes in

shape we measured for *N. luetkeana*. Similarly, *Dictyota* sp. developed wider blades when they were experimentally protected from water flow (Stewart and Carpenter 2003). When transplanted from wave-swept to protected sites, *T. ornata* developed pneumatocysts (Stewart 2006a). The blades of *M. integrifolia* from sites exposed to different flow regimes converged to the same morphology after being transplanted into one site (Druehl and Kemp 1982). In contrast, other species of macroalgae, such as *Eisenia arborea* (Roberson and Coyer 2004) and *Sargassum cymosum* (De Paula and De Oliveira 1982) that show morphological differences correlating with flow habitat, did not change when transplanted, suggesting genotypic differences between populations at different sites.

The morphological plasticity of some macroalgae should enable them to adjust their form to the local flow environment they experience as neighboring organisms grow around them and alter the movement of ambient water. Kelp beds and other algal canopies reduce current velocities and attenuate waves (Koehl and Alberte 1988; Dudgeon and Johnson 1992; Elwany et al. 1995; Jackson 1997; Koehl 2000; Boller and Carrington 2006b; Gaylord et al. 2007; Rosman et al. 2007). Such differences in local flow characteristics caused by neighboring organisms should be reflected in the morphologies of seaweeds within the bed. We found that blades of *N. luetkeana* at the edges of the TR kelp bed that were exposed to the most rapid flow were only ~3 cm wide, whereas those at the more sheltered middle of the bed were wider (mean width 4.4 cm) (Koehl and Alberte 1988).

Based on their study of morphological plasticity in barnacles, Li and Denny (2004) argued that limits to the range of morphologies that members of a species can assume restrict the range of habitats in which that species can survive. Because we did not expose *N. luetkeana* to velocities higher than those encountered at our field sites, we do not yet know the limit on their capacity to alter blade shape.

The rates at which phenotypically plastic organisms can change their structure affects their survivorship if they live in unpredictable, temporally variable environments. Palumbi (1984) argued that survivorship can be enhanced if phenotypically plastic organisms alter their morphology quickly when an environmental change carries high risk for the inappropriate morphology, but respond more slowly if the risk of mortality of the wrong morphology is low. Specifically, selection should favor rapid phenotypic responses to increased exposure to fast flow or to waves, and slow responses to reduced flow. Reciprocal transplant

experiments with the macroalga *Ecklonia radiata* showed that individuals that had been moved from protected to exposed habitats changed their morphology rapidly, whereas those transplanted from exposed to protected sites altered their form more slowly (Fowler-Walker et al. 2006). Our 6-day experiments hint at a similar asymmetry of response rates for *N. luetkeana*: the changes in shape of protected-morph blades subjected to exposed-site loads (Fig. 11A) were much more pronounced than were those of exposed-morph blades subjected to protected-site loads (Fig. 11B).

Morphological responses that occur over a period of days cannot protect an organisms from sudden increases in ambient flow that can occur over a period of a few hours when a storm hits or when an organism is transplanted from a protected to an exposed habitat. Duggins et al. (2001) found higher mortality rates for *N. luetkeana* living at sites exposed to long periods of calm “punctuated by periods of strong currents” than they did at sites consistently exposed to very rapid flow (*N. luetkeana* in the former habitats had probably assumed a ruffled morphology during the long periods of calm, whereas those at the exposed sites were no doubt flat and strap-like). Similarly, a number of studies of macroalgae showed that individuals with the slow-flow morphology washed away when transplanted to habitats exposed to rapid flow of water, whereas thalli with fast-flow morphologies transplanted to protected habitats survived (Chapman 1974; Gerard and Mann 1979; Stewart 2006a). Storms tend to occur seasonally. Therefore, for those individuals that survive the first storm of the season, a change in morphology that occurs over a period of days should enhance their chances of surviving subsequent storms.

Growth rates of blades of different shapes

Growth rates of blades of *N. luetkeana* in our experiments were faster for ruffled blades than for strap-like blades when the kelp grew in their natural habitats (Fig. 3), and when they grew together in laboratory tanks (compare Fig. 11A and B). Furthermore, in the latter experiments, the blade on an individual that grew with no weight (and hence became ruffled) elongated more rapidly than the blades on that individual that bore weights (and hence became strap-like). This was true both for the ruffled individuals from the protected site (Fig. 11A) and for the strap-like individuals from the exposed site (Fig. 11B). One factor that might contribute to the slower elongation rates of strap-like blades is that they are thicker than ruffled blades: a unit volume of

new growth produces a smaller increase in blade area for a thick blade than for a thin one. Another factor that might contribute to the difference in growth rates between ruffled and flat blades is the ability of ruffled blades to avoid self-shading. Genetic differences between the individuals collected from the protected site versus from the exposed site might also have contributed to the differences in growth rates between ruffled and flat blades. Further study is needed to resolve this issue.

Mechanical cues induce changes in growth patterns

Our laboratory experiments in which growing blades of *N. luetkeana* from exposed and protected sites were subjected to tensile forces that mimicked the drag experienced by blades in different flow regimes showed that change in shape was induced by mechanical stress. Some evidence indicates that the growth of other species of macroalgae also respond to mechanical cues. Gerard (1987) found similar changes in shape when she hung weights on growing blades of *Laminaria saccharina*. Furthermore, mechanical cues have been shown to affect cells of the kelp *Egregia menziesii*: stretched tissues increased their rate of C_{14} incorporation and synthesis of cell walls (Kraemer and Chapman 1991a), enhanced their production of structural compounds (Kraemer and Chapman 1991b), and increased the crystallinity of their cell walls (Hackney et al. 1994).

Many types of vascular plants change their shape in response to mechanical loads (“thigmomorphogenesis,” reviewed in Jaffe et al. 2002). For example, it has long been known that wind loading leads tree trunks to develop an optimum shape for stability under wind drag (Leiser and Kemper, 1973). Similarly, wind affects the resistance to bending (stiffness) of herbaceous plants by influencing the shape of the stems (Py et al. 2006). The role of mechanical processes in plant morphogenesis is well-documented (reviewed by Braam 2005; Schopfer 2006; Dumais 2007). For example, in higher plants the most common morphogenesis in response to mechanical loading by wind involves the slowing of elongation and an increase in radial growth rate. The amount of longitudinal mechanical strain imposed on a plant stem is strongly correlated to the magnitude of its thigmomorphogenetic response. Furthermore, younger tissues are most responsive to mechanical stimuli, but deformations imposed on older tissues can generate a morphogenetic response in distant younger tissue (Coutand et al. 2000).

Ways in which cellular processes affect plant shape are also being elucidated. For example, flat snapdragon

leaves become ruffled when mitotic arrest occurs later in the leaf margins than along the leaf midline, and the margins subsequently grow more than the leaf center (Nath et al. 2003). This suggests a possible link to kelp ruffle formation, since high growth rates occur in the regions of kelp blades where the activity of cytokinin is highest (de Nys et al. 1990), and cytokinins promote cell division. However, cell division (which is the partitioning of existing volume) does not lead to growth unless it is synchronized with cell expansion. Although the basic mechanism linking rapid cell expansion to a recent division event remains to be elucidated, it is known that local expansion of plant tissues depends on mechanical yielding of the cell walls, which in turn depends both on their micro-architecture and on the mechanisms by which their yielding properties are controlled (reviewed by Baskin 2005; Cosgrove 2005).

Much also has been learned about how mechanical signals affect molecular processes within cells (reviewed by Trewavas 1999; Braam 2005; Vogel and Sheetz 2006). Genomic responses to touch are extremely prevalent. For example, over 2.5% of the *Arabidopsis* genome is upregulated within 30 min after a mechanical stimulus, and another 0.75% is downregulated (Lee et al. 2005). Many of the upregulated genes are Ca^{+2} -binding proteins or proteins involved in modification of the cell wall. Two models have been proposed for transduction of a mechanical strain signal at the cellular level: (1) stretch-activated channel activity may trigger ion fluxes during mechanical perturbation of the membrane, or (2) tethered transmembrane proteins may perceive mechanical stimuli and influence the cytoskeleton or trigger ion fluxes that act as secondary messengers. An example of the latter is Ca^{+2} , which is either released from intercellular stores or is imported from a bathing medium (possibly interacting with reactive oxygen species). Such Ca^{+2} functions as an intracellular messenger both in signaling a mechanical stimulus and in cell responses to such signals. Iwabuchi et al. (2008) have concluded that a change in membrane tension is the most important activator of the mechanosensitive Ca^{+2} channel in *Charales*. Although information about such processes in *N. luetkeana* is not yet available, it is known that calcium is released from a green alga, *Nitella*, in response to mechanical stretching.

Other environmental cues that might induce changes in macroalgal morphology

Local changes in growth patterns of *N. luetkeana* blades might also be induced by other environmental

cues in addition to mechanical stress. For example, strap-like blades at exposed sites experience a higher degree of self-shading, and hence lower photon flux densities, than do ruffled blades in protected habitats. Furthermore, water flow across blade surfaces affects rates of uptake of materials such as bicarbonate, dissolved gases, and nutrients, which in turn affect photosynthesis, respiration, and growth (reviewed by Hurd 2000). Fine-scale local differences in mass exchange rates along blade surfaces might affect growth rates in particular regions of blades. Studies of gamete release by macroalgae have shown that algal cells can respond to local levels of flow-enhanced mass exchange (Pearson et al. 1998; Gordon and Brawley 2004). The responses of the patterns of growth and shape of the blades of *N. luetkeana* to differences in light or nutrients remain to be studied.

Some changes in seaweed morphology that occur at exposed sites are induced by damage. For example, the higher branching of a number of species of algae at exposed sites is the result of regrowth by thalli that have been tattered by waves (Haring and Carpenter 2007). The smaller size of individuals at sites exposed to rapid flow can be due to “pruning” of distal portions of the thalli that are ripped off by waves (Black 1976; Blanchette 1997). Damage can also induce a macroalga to increase the strength and toughness of its tissues (Lowell et al. 1991).

Conclusion

Like many species of macroalgae, *N. luetkeana* have narrow, thick, flat blades at sites exposed to rapidly flowing water, but have wide, thin, ruffled blades in sheltered habitats. Strap-like blades collapse into streamlined bundles in flowing water, thus reducing both drag and interception of light, while ruffled blades remain spread out in moving water, thus experiencing high drag but little self-shading. Ruffles are produced by elastic buckling when rates of longitudinal growth at the edges of a blade exceed the rate of longitudinal growth along the midline. Transplant experiments in the field revealed that shape of the blades in *N. luetkeana* is a plastic trait, and laboratory experiments showed that this change in shape is induced by mechanical stress. Our study of ecomorphological differences in the shapes of blades of *N. luetkeana* in different flow habitats illustrates how plastic growth responses to the mechanical cues experienced by organisms can generate body forms that perform well in their local flow environments.

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