Journal of Experimental Marine Biology and Ecology 340 (2007) 227 – 246

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

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# Biomechanical factors contributing to self-organization in seagrass landscapes

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Received 6 March 2006; received in revised form 20 June 2006; accepted 20 September 2006

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## Abstract

Field observations have revealed that when water flow is consistently from one direction, seagrass shoots align in rows perpendicular to the primary axis of flow direction. In this study, live *Zostera marina* shoots were arranged either randomly or in rows perpendicular to the flow direction and tested in a seawater flume under unidirectional flow and waves to determine if shoot arrangement: a) influenced flow-induced force on individual shoots, b) differentially altered water flow through the canopy, and c) influenced light interception by the canopy. In addition, blade breaking strength was compared with flow-induced force to determine if changes in shoot arrangement might reduce the potential for damage to shoots.

Under unidirectional flow, both current velocity in the canopy and force on shoots were significantly decreased when shoots were arranged in rows as compared to randomly. However, force on shoots was nearly constant with downstream distance, arising from the trade-off of shoot bending and in-canopy flow reduction. The coefficient of drag was higher for randomly-arranged shoots at low velocities ($<30$ cm s$^{-1}$) but converged rapidly among the two shoot arrangements at higher velocities. Shoots arranged in rows tended to intercept slightly more light than those arranged randomly. Effects of shoot arrangement under waves were less clear, potentially because we did not achieve the proper plant size–row spacing ratio. At this point, we may only suggest that water motion, as opposed to light capture, is the dominant physical mechanism responsible for these shoot arrangements. Following a computation of the Environmental Stress Factor, we concluded that even photosynthetically active blades may be damaged or broken under frequently encountered storm conditions, irrespective of shoot arrangement.

We hypothesize that when flow is generally from one direction, seagrass bed patterns over multiple scales of consideration may arise as a cumulative effect of individual shoot self-organization driven by reduced force and drag on the shoots and somewhat improved light capture.

*Keywords:* Currents; Drag; Environmental safety factor; Flow; Landscape pattern; Light; Seagrass; Self-organization; Waves

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## 1. Introduction

We have observed that seagrass shoots align in rows, much like planted crops, perpendicular to the flow (whether unidirectional or oscillatory) when the flow is consistently on a constant axis of direction. We have

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doi:10.1016/j.jembe.2006.09.015

observed this phenomenon at a number of geographic locations, and for several species: *Zostera marina* (Ninigret Pond, Rhode Island; San Francisco Bay), *Halodule wrightii* (Tampa Bay, Florida; Puerto Morelos, Mexico; Culebra Island, Puerto Rico [J. Rivera, NMFS, NOAA, pers. Com]), *Posidonia kirkmanni*, *P. robertsonii*, *P. coriacea*, *P. augustifolia*, *Amphibolis* spp., and, to a lesser degree, *Halophila* spp. (Two Peoples Bay, Western Australia) (Fig. 1). One common aspect of the physical setting of all these situations has been that water flow tended to be aligned in a consistent direction and that row formation occurred perpendicular to the axis of that flow direction. These observations indicate that many seagrass species respond to these flow conditions with a systematic self-organization of shoots on the sea floor, but the consequences of this arrangement were unclear. It has been suggested (H. Kirkman, CSIRO, Perth, Australia, pers. com.) that some seagrasses form rows because their seeds were entrained in sand ripples that also form perpendicular to flow direction. However, brushing the sand away from the rhizomes in some of these beds reveals that those rhizomes (a post-germination structure) also extend across the bottom normal to the flow as well.

Self-organization of sessile communities is not limited to examples from seagrass. van de Koppel et al. (2005) report on mussel bed patterning that also aligns generally perpendicular to ambient flow direction. Using a simple spatial simulation model, they demonstrated that such a pattern can arise from short-range facilitation among the bivalves by mutual sheltering from waves and currents as well as long-range competition for algae (food). One mechanism not emphasized in that study was the role of downstream turbulent wakes in controlling

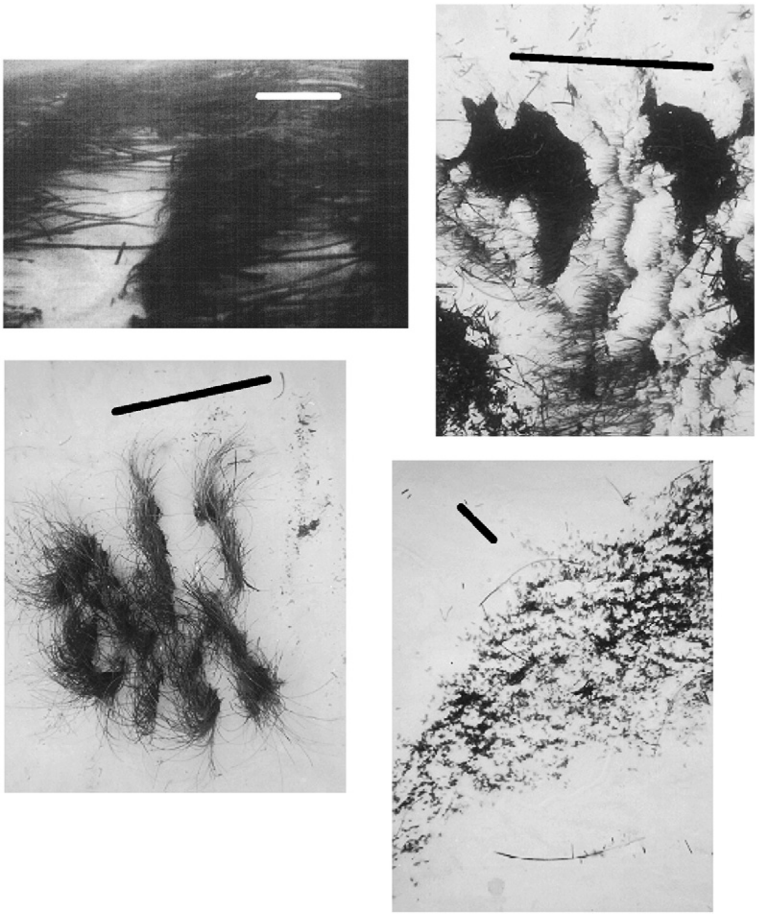

Fig. 1. Photographs of seagrass beds showing row formations (clockwise from upper left). The direction of water flow is indicated by the orientation of the scale bars. A. *Zostera marina*, Charlestown Pond, Rhode Island (scale bar = 0.10 m). B. *Heterozostera tasmanica*, Two Peoples Bay, Western Australia (scale bar = 1.0 m). C. *Posidonia coreacea*, Two Peoples Bay, Western Australia (scale bar = 0.10 m; note loss of row formation to the right of the picture). D. *Posidonia coreacea*, Two Peoples Bay, Western Australia (scale bar = 1.0 m).

pattern scale, as argued by Folkard (2005) for *Posidonia oceanica* patches. Similarly, the relation of marsh pattern self-organization (van de Koppel et al., 2005) to instability (certain self-organized patterns may eventually presage marsh collapse) bear an intriguing resemblance to the observations of Duclos and Clement (2004) where subtle changes in object spacing can dramatically increase or decrease wave forces on rigid columns. Taken all together, these observations strongly infer that self-organization of sessile organisms is a common mechanism for coping with gradients of limiting factors in a variety of ecosystems— however, to our knowledge this has never been quantitatively examined in seagrass ecosystems.

Consideration of the clonally integrated growth and colonization strategies of seagrasses may also provide some clues as to the potential importance of shoot arrangement in seagrass bed maintenance and expansion. Some seagrasses, such as *Z. marina*, vegetatively colonize new areas with shoots that move across the sea floor (i.e. individual shoots actually migrate via vegetative extension) over short periods of time (weeks). In contrast, other seagrasses (e.g., *H. wrightii*, *Thalassia testudinum*) have shoots that are rooted in place while an adventitious plagiotropic shoot (a modified rhizome) grows away across or under the seafloor, colonizes new space and gives rise to new, immobile orthotropic shoots. We posit that seagrasses whose shoots change position over time may have a better opportunity to reorganize their spatial arrangement in direct response to environmental conditions. Moreover, clonal plants such as seagrasses, often integrate resources among the individual shoots (Terrados et al., 1997); thus, clonal integration creates the potential for physiological feedback that could register and transmit any benefit of shoot arrangement to individuals comprising the clonal unit. Therefore, the potential for ecologically advantageous and rapid spatial rearrangement may exist for at least some seagrass species such as *Z. marina*. Despite studies that evaluate the effects of the size of seagrass beds on flow reduction within the canopy (Fonseca et al., 1983; Worcester, 1995; Peterson et al., 2004; Folkard, 2005; Fonseca and Koehl, 2006) the consequences of shoot arrangement have not been studied.

Although the potential consequences of shoot arrangement in seagrass beds have not been addressed, the importance of other biomechanical attributes bears on their ability to respond to drag forces. For example, plant flexibility should also decrease flow-induced force on individual shoots. Flexibility reduces the area presented to the flow and under waves, allows the plant to move with the flow, minimizing the time that flow is accelerating past the plant thereby reducing drag, especially under waves. The flexibility of seagrass canopies is extreme (Fonseca and Kenworthy (1987) predict that *Z. marina* canopy height/shoot height ratio will be reduced ~85% at 0.55 m $s^{-1}$) in comparison to terrestrial crops such as grains, that would buckle at that deflection (Niklas, 1992). Moreover, by bending over synchronously as seagrass canopies do, the biomass of the canopy is concentrated near the sea floor exacerbating near-sediment velocity reduction and likely, the force experienced by individual shoots (Fonseca et al., 1982; Gambi et al., 1990; Abdelrhman, 2003). It may be that one of the reasons that shoot density has not been shown to have a strong effect on flow reduction in seagrass canopies is because the shoots are so highly flexible. It is well known that both plants and animals (Charters et al., 1969; Koehl, 1976, 1977, 1986; Denny et al., 1985; Denny, 1988; Koehl and Alberte, 1988; Carrington, 1990; Abdelrhman, 2003; but see Peterson et al., 2004) experience reduced drag as the result of bending with increasing flow. Thus, the inherent flexibility of many aquatic species may make it difficult to isolate stem spacing effects on flow for comparison with terrestrial ecosystems.

Plant stem density, flexibility, and leaf area have all been evaluated for their influence on flow, yet to our knowledge, no studies of the effect of plant arrangement on canopy flow interactions have been conducted in aquatic systems when the plants were highly flexible. However, wind tunnel studies have shown that changes in the spacing of rigid shoot mimics does affect the drag coefficients of individual elements (cylinders; Marshall, 1971). Drag, as computed from velocity profiles, did not vary substantially within a limited range of spacing arrangements (i.e., clumped, random, uniform) while holding a constant density of elements (Marshall, 1971). Marshall (1971) concluded that randomly distributed elements would be expected to exert less drag on the passing flow than other arrangements, and that a single row of elements aligned across the flow exert greater drag than if the same elements were arranged parallel to the flow. Like the aforementioned study by Duclos and Clement (2004), the geometry of rigid mimic arrangement can itself influence canopy flow interactions— but does this hold for highly flexible seagrasses?

Bending and mutual sheltering have also been shown to decrease light transmission through plant canopies, possibly to the detriment of plants that are overlapped by neighbors (Short, 1980; Holbrook et al., 1991). Although there has been extensive work on the physiological ecology of seagrasses (see reviews: Zieman, 1982; Thayer et al., 1984; Phillips, 1984; Zieman and Zieman, 1989), only a few studies describe the relationship between seagrass canopy deformation and resultant self-shading and photosynthetic inhibition (Dennison, 1979; Dennison and Alberte, 1982). These studies indicate that increased bending and layering of the canopy may reduce the total amount of light available to the plants. These studies, however, were conducted under nearly static flow conditions (compared to the flow conditions used in this study) with the result that variation in their measurements of light capture efficiency did not account for any influence of canopy movement (e.g. "Honami" Fonseca and Kenworthy, 1987 or "Monami"; Grizzle et al., 1996) on light availability to the plants. Koehl and Alberte (1988) and Holbrook et al. (1991) concluded that a reduction in light capture with increasing flow occurs as plant shape becomes more streamlined and blades mutually shade each other. However, given that some seagrass species are capable of altering the position of their shoots on the sea floor (e.g. *Z. marina*), then self-organization could be a mechanism that would allow shoots to arrange in a pattern that improved light capture despite local hydrodynamic conditions that would otherwise cause them to mutually shelter one another.

A shoot's breaking strength is another factor that could influence shoot arrangement pattern. If a change in shoot pattern resulted in lower flow-induced force on a plant, then that change would favor maintenance of beds at that location, as well as plants or plant tissue with lower breaking strength, presumably at lower physiological cost. Patterson et al. (2001) tested reproductive shoots of *Z. marina* and found that reproductive shoots could absorb high levels of strain before failure. There is also some evidence from brown algae that links plant growth to flow-induced force. Johnson and Koehl (1994) demonstrated that growth responses by the giant kelp (*Nereocystis luetkeana*) are sufficient to hold constant ratio of stress relative to strength in the plant's tissue under various flow regimes (Environmental Stress Factor: the ratio of the stress required to break a component of an organism [in this case the stipe] at some stage in its life to the maximum stress normally encountered in the habitat by that component during that stage). It is unknown whether seagrasses exhibit this ability. Moreover, we are not aware of any published information as to whether seagrass breaking strength is at all near to that experienced in nature (but see Kopp, 1999 where breaking and uprooting forces may approach damaging levels and the work of Patterson et al. (2001) that suggests some individuals may be exceptionally resistant to damage). Therefore, the potential interrelationship of flow-induced force, light capture and breaking strength with shoot arrangement, if any, remains unexplored. We also posit that the existence of any biomechanical relationship between flow, self-organization and plant breaking strength at the individual shoot scale could be a fundamental process influencing the expression of larger scale (meters— 100's of meters) patterns observed in seagrass beds.

Understanding the proximal cause of pattern formation in seagrasses is useful not only for planning restoration projects (Fonseca et al., 1998a,b), but is also relevant to other ecological processes, such mediation of predator–prey interactions and facilitating species coexistence (van de Koppel et al. 2005 and references therein), although further discussion on the significance of that in seagrasses is beyond the scope of this paper. Nonetheless, self-organization in ecosystems and its ecological function is an emerging attribute of landscape studies (Levin 1992; Guichard et al. 2003; Rietkerk et al., 2004; van de Koppel et al., 2005).

### *1.1. Study purpose*

Here, we ask here whether a particular shoot arrangement might confer some ecological advantage to these clonal plants. To summarize; self-organization of seagrass shoots could potentially confer some ecological advantage to the plants through:

- Reduction of flow-induced force on individual shoots or shoot components (and thus, damage to shoots),
- Reduction of sediment erosion in the rhizosphere, and
- Increased light capture ability by the leaf canopy.

Therefore, in order to evaluate the ecological significance of seagrass self-organization in nature, the relationship between water flow, flow-induced force, plant breaking strength, light capture and plant arrangement was assessed under laboratory conditions, using a well-studied seagrass (eelgrass, *Z. marina* L.). Specifically, we asked:

- Does shoot arrangement influence flow-induced force on individual shoots?
- Does shoot arrangement differentially influence within-canopy flow?
- Does shoot arrangement influence light capture by the canopy, and,
- How does the breaking strength of these plants relate to that experienced under waves and currents typical of that found in their local habitat?

## 2. Materials and methods

### 2.1. Experimental apparatus

Experiments were conducted in a seawater flume at the NOAA Laboratory in Beaufort, NC. The flume was 8 m long × 1 m wide × 0.75 m deep and was modified from a design presented in Vogel (1994). The upstream end of the flume was fitted with collimators (tubes that were 1.0 m long × 0.1 m diameter) to smooth the flow and reduce turbulence (Nowell and Jumars, 1987). Current velocity over the test section (which was 1 m long and was located 2 m downstream from the collimators) could be varied from 0.05 to 1.0 m $s^{-1}$, depending on water depth. Unidirectional currents were generated by two stainless steel propellers in tandem (0.4 m diameter × 0.305 m pitch) driven by a two-horsepower DC motor fitted with a 5:1 reduction gear, mounted vertically on a 2.54 cm diameter shaft, so that the propellers were within the return pipe where it exited the floor of the flume, downstream of the test section. Water was pushed through a 45 cm diameter pipe mounted under the flume body to the opposite end, where it re-entered the flume vertically, through the floor of the flume, upstream of the collimators.

The flume was designed with removable components that allowed switching between unidirectional flow and waves. Waves were generated using a paddle that spanned the width of the flume (after Fonseca and Cahalan, 1992). The paddle was moved back and forth by a 0.5 horsepower DC motor. Wave height and period could be controlled by changing the length of the armature between the motor and the paddle and by adjusting belts connecting the motor to the armature. Wave energy was absorbed at the end of the flume away from the paddle generator by a sloping beach and plastic mesh.

Water was drawn from the estuary through the Laboratory seawater system to fill the flume; water in the flume maintained a constant temperature of 22.5 °C and a salinity of 34 ppt. The still water depth of water in the flume (0.25 m) represents a typical low tide water depth over local *Z. marina* beds near Beaufort (authors' pers. obs.).

### 2.2. Seagrass

We used *Z. marina* L. plants to study the effects of shoot arrangement on hydrodynamic forces and light capture by seagrass. Plants were collected from Middle Marsh (34° 42′ N × 76° 37′ W) in the Rachel Carson National Estuarine Research Reserve by digging up small sods and gently rinsing sediment away from the root and rhizome mass. Plants were transported to the laboratory in a seawater-filled cooler and maintained in flowing seawater tanks at ambient temperature (~27 °C) and salinity (34 ppt) for ~24 h prior to their use in any of the experiments described below.

### 2.3. Force transducers

Seagrass buoyancy, flexural stiffness, and flow-induced force on individual seagrass shoots were measured in all experiments with temperature-compensated force transducers, modeled after those described by Koehl (1977) and Vogel (1994). A transducer was constructed by bonding a foil strain gauge to each side of a 13 × 60 mm force beam made of stainless steel shimstock. The thickness of the shimstock affected transducer stiffness, and hence its sensitivity; we used shimstock ranging in thickness between 0.051 to 0.152 mm to obtain a range of sensitivities. The base of the shimstock was embedded in epoxy within an acrylic mount. An aluminum tube (the "sting") 1.5 mm in diameter was epoxyed on the free end of the shimstock for attachment of seagrass shoots. The force transducer was then waterproofed, first with 3 coats of wax and then 3 coats of nitrile rubber.

When applications would be in water, transducers were calibrated (0.001 N precision) after soaking overnight in seawater, otherwise they were calibrated after 24 h in air after a fresh water rinse. Calibration was performed for deflection in both directions for each force transducer, using the technique described in Emerson and Koehl (1990). The soaked force transducer was mounted with its sting pointing down and a thread attached to the distal portion of the sting where the seagrass shoots would be attached. The thread was passed over a pulley at a 90° angle to the transducer. Factory certified, analytical quality weights for use in calibrating balances were then attached in random order to the thread, providing a range of forces from 0.001 to 0.050 N ($n=6$).

For measuring force, wire leads from the force transducer were attached to a Vishay Model p-3500 Strain Indicator using a half bridge configuration to compensate for temperature effects on transducer strain. Data were recorded using LABTECH® software (version 8.1) on an Ambra® laptop computer at an acquisition rate of 50 Hz. The correlation coefficient for the linear regression of Strain Indicator output on force was always greater than 0.99 for all the transducers used in this study. Force transducers were rechecked periodically for consistency and linearity of response and rejected if $r<0.99$.

### 2.4. Plant flexural stiffness and buoyancy

The influence of light and temperature on seagrass flexural stiffness buoyancy and flexural stiffness was determined prior to conducting the flume experiments (see below). Seagrass blades can store gases in their lacunae as the result of photosynthesis (Penhale and Wetzel, 1983). Because such gas storage might affect blade buoyancy, and hence how far blades are bent over in flowing water, any effect of light on stiffness and buoyancy (and thus, flow-induced force on the plants) had to be determined before experiments on shoot arrangement were conducted, especially if light conditions in the flume were sub-optimal. Similarly, because the stiffness of biological tissues can change with temperature (e.g. Wainwright et al., 1976), the flexibility of shoots, and hence the flow-induced force (e.g., Koehl, 1986), might change if temperature in the flume varied. Flexural stiffness was examined on plants held under saturating light conditions (~450 μ Einsteins $m^{-2}$ $s^{-1}$) from a halogen flood lamp designed to produce a light spectrum similar to that required by chl a (Philips 250 W model: K250PARFL) and on plants held in darkness, each for 48 h and both in gently flowing seawater ensuring ambient temperatures. Based on laboratory observations where the oxygen evolution rate for seagrasses stabilizes within 16 min to changes in light intensity (Dennison and Alberte, 1986; Kenworthy, 1992), a 48 h period was chosen for our experiment to ensure a stable photosynthetic rate was maintained by the plants in the light and that oxygen evolution had ceased for plants in the dark.)

For a seagrass blade being bent like a cantilevered beam by a point load,

$$EI = (F{*}L^3)/8\ \delta \qquad (1)$$

where: $E$ is the modulus of elasticity (N $m^{-2}$) of seagrass tissue, $I$ is the second moment of area ($m^4$) of the cross-section of a bending seagrass blade ($I = b\,d^3/12$) for a shape rectangular in cross-section, where $b$ = width of the blade and $d$ = thickness of the blade), $F$ is the force (N) applied at a point along the cantilever, $L$ is the distance between the point of force application and the attached end of the blade and $\delta$ is the deflection distance (m) of the point on the blade where the force is applied (Eq. (1) can be used when $\delta < 0.10$ L [e.g. Wainwright et al., 1976; Niklas, 1992], a criterion that was maintained for all measurements).

Buoyancy was also measured in the laboratory on plants held in saturating light for 48 h by attaching whole plants, detached from the rhizome at first discernable root node, to a force transducer and recording the force per unit volume of the floating blade.

### 2.5. Shoot arrangement

Two shoot spacing arrangements were compared in the experiments described below: a) shoots in rows or b) shoots arranged randomly. Six experimental trials (3

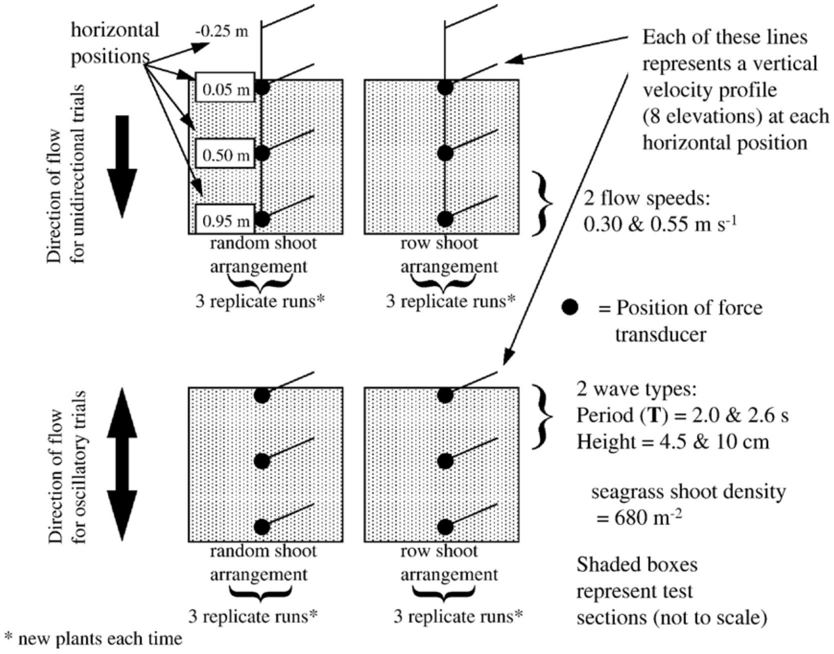

Fig. 2. Diagram of experimental design used in flume studies of unidirectional flow, waves and canopy light capture.

replicates per shoot arrangement) were conducted. In each trial, hydrodynamic force on individual shoots, velocity profile, and light interception by the seagrass canopy were measured at the same defined positions in the flume (Fig. 2). Shoot density was held constant at 680 $m^{-2}$ to approximate the average maximum density of *Z. marina* measured during the spring in Core and Back Sounds, Carteret County, North Carolina (latitude 34:40–34:50 ° N, longitude 76:20–76:40° W; Fonseca and Bell, 1998). To approach consistency with past studies (Gambi et al., 1990) and based on scaling assessments by Fonseca and Koehl (2006), the seagrass bed constructed for the flume experiments was 0.25 m wide by 1.0 m long. Clear acrylic plates the size of the test section were fit into a recessed portion of flume floor so as to be flush with the main floor of the flume. Random arrangements of shoots were created in the lab by overlaying the plates with a clear plastic grid (grid intersections on 1 cm centers) numbered 1–2500 and then choosing 170 random locations in that range. Holes (6.25 mm diameter) were drilled through the plate at these points and *Z. marina* shoots were wedged through each hole in a naturally upright position so that the plate surface intersected the shoot at the same position as the sediment surface intersected the shoot in the field. Freshly-harvested plants from nearby Back Sound were used for each trial; shoots were not re-used.

Row arrangement was determined by examining the relationship between shoot length and row spacing captured in photographs of five genera (*Amphibolis*, *Halophila*, *Heterozostera*, *Posidonia*, *Zostera*; author's unpubl. data). From this arbitrary photographic sample, the percent overlap was computed for *Z. marina* and *Heterozostera tasmanica*, the only another strap-blade species for which photographs were available. Blades overlapped from 25 to 50% of the neighbors in the next row and rows in this experiment were created to have 50% overlap (170 shoots arranged in 9 rows with 19 to 21 shoots in each). After each replicate of a shoot arrangement treatment was run, 30 shoots were randomly selected for measurements of blade and stem length, width, and thickness (measured to the nearest 0.01 mm using digital calipers).

### *2.6. Flow conditions and measurements*

Each replicate of each shoot arrangement was subjected to two unidirectional current velocities and two wave conditions (Fig. 2). The two unidirectional current velocities used, 0.30 and 0.55 m $s^{-1}$, were measured at the horizontal position of −0.25 m, which was 0.25 m upstream of the grass bed (Fig. 2). The mean velocity at this horizontal position was calculated by taking the arithmetic mean of the mean time-averaged velocities measured at different heights above the substratum, as described below. Mean velocities of 0.30 and 0.55 m $s^{-1}$ were chosen to represent moderate and high velocities measured just upstream of *Z. marina* beds in the field near sites from which the plants used in the flume were collected (Fonseca et al., 1983, unpubl. data). These velocities were selected so that the grass shoots in the flume would experience large hydrodynamic forces and would be bent over to varying degrees parallel to the flow, allowing a range of combinations of drag force on shoots and light interception by the canopy.

The two wave conditions used in our experiments were: 1) a wave period of 2.0 S and a wave height of 0.045 m, and, 2) a wave period of 2.6 S and a wave height of 0.10 m. These wave heights and periods were slightly greater than the average found over seagrass beds in the Beaufort area (period range of 0.6– 3.0 S, 1.6 average; height range 0.01–0.20 m, 0.06 average; Fonseca and Cahalan, 1992). Rather, these values were selected because flexible plants move back and forth with the water that oscillates to and fro under waves; if the length of a shoot is smaller than the distance the water travels in one direction before it reverses, then the shoot will become fully extended in the direction of the flow (Koehl, 1986, 1989). In our experiments, shoots were fully extended in the waves of period 2.6 S, but not in the waves of period 2.0, allowing a comparison of shoots in tension and not in tension.

For the two unidirectional flow conditions, vertical profiles of velocity were recorded at four horizontal positions along the centerline of the flume; 0.25 m upstream of the edge of the grass bed and 0.05, 0.50 and 0.95 m downstream from the upstream edge of the grass bed (Fig. 2). At each of the horizontal positions described above, velocity was measured at heights of 0.02, 0.05, 0.08, 0.11, 0.14, 0.17, 0.20 and 0.23 m above the substratum using a Marsh-McBirney model 523 two-axis electromagnetic current meter. All velocities reported here represent the resultant of these two velocity vectors. The time constant on the current meter was set to its highest resolution (0.2 s). The water current velocity probe head was 0.0125 m diameter. The probe was mounted vertically in a bracket which was raised or lowered to the eight preset elevations above the bottom. Current velocity was recorded on a laptop computer using LABTECH® software (version 8.1) at 50 Hz for 30 s at each of the eight elevations above the substratum bottom and at each of the horizontal positions in the flume. Signals from the various sensors (flow meter, force transducer and light meter— see below) interfaced with the computer through an analog-digital conversion board (Computer Boards Inc., model CIO-DAS08). Vertical profiles of velocity were also recorded for each horizontal position under all four hydrodynamic regimens (two unidirectional velocities and two wave conditions) when no grass shoots were in the flume.

### 2.7. Reynolds number

For each position along the tank at which there was seagrass, bulk flow Reynolds number ($Re_b$) (*sensu* Gambi et al., 1990) was calculated:

$$Re_b = U_b L_b / v \tag{2}$$

where $U_b$ is the arithmetic mean of the mean time-averaged velocities from all eight elevations at that position (m s$^{-1}$), $L_b$ is a characteristic length (in this case, water depth [m]), and $v$ is the kinematic viscosity of seawater (m$^2$ s$^{-1}$) at 20 °C ($1.047 \times 10^{-6}$). Reynolds number represents the relative importance of inertia to viscosity for a particular flow situation and allows scaled and thus, unbiased comparisons of flow conditions among trials.

### 2.8. Flow velocity in the canopy relative to upstream flow

Change in the current velocity was analyzed using both actual velocities as well as a percent of velocity upstream of the bed. Velocity data (both actual and percent changed) were examined under three-way ANOVA for effects above and within the canopy, with main effects of downstream distance, flow regime and shoot arrangement. The mean current velocity (time-averaged) at each elevation for each horizontal position within the test section was divided by the mean current velocity (time-averaged) at the same elevation measured 0.25 m upstream of the test section and multiplied by 100. These mean percent flow velocities were arcsine-transformed prior to analysis under ANOVA.

During oscillatory flow, in each wave cycle a peak velocity was reached in one direction (+) along the flume and in the opposite direction (−) along the flume. For each oscillatory flow treatment, the mean of the absolute values of all the peak velocities in both directions was calculated for each elevation in a velocity profile at each horizontal position within the seagrass test section. The average of the maximum velocities for all the elevations at a horizontal position was calculated (arithmetic mean among elevations). Because seagrass blades wave back and forth in oscillatory flow, the height of the canopy changed with time, and every elevation at which flow was measured was within the canopy for part of the wave cycle. Therefore, the percent maximum velocities of all the elevations were averaged for each horizontal position. These percent maximum velocities were arcsine-transformed and tested using three-way ANOVA with main effects of downstream distance, wave type and shoot arrangement.

### 2.9. Turbulence intensity

For each 30 S velocity record in unidirectional flow, the mean velocity and the mean turbulence intensity ($U_{\mathrm{rms}}$, the root mean square of velocity measurements) were calculated. Turbulence intensity was calculated following Gambi et al. (1990):

$$U_{\mathrm{rms}} = (\mathrm{rms}U / \hat{u}) \times 100 \tag{3}$$

where: rms$U$ is the root mean square of the velocity (in our case measured at 0.02 s intervals for a duration of 30 s computed using RMSE function in SAS®) and $\hat{u}$ is the mean (time-averaged) velocity at each height. In these control experiments, for each of the four flow conditions used, the mean velocities and turbulence intensities were calculated for each height above the substratum at each horizontal position. Turbulence intensity was examined under three-way ANOVA for effects above and within the canopy, with main effects of downstream distance, flow regime and shoot arrangement.

In our oscillatory flow treatments, the mean velocity changed with time in a sinusoidal manner as the water flowed back and forth at the defined frequency in the tank. In these cases, $U_{\mathrm{rms}}$ was calculated using the deviations ($U'$) from the mean sinusoidally-varying velocity. A Box–Jenkins differencing procedure (Parkantz, 1983) was used to extract the velocity fluctuations at the period of the wave prior to computation of $U_{\mathrm{rms}}$. The procedure first measures the periodicity of the peaks in velocity (which in this case was the wave's periodic velocity signature), then subtracts the observed velocity from that velocity predicted at each time increment by an ideal sine wave of that period and amplitude. Left are velocities that depart from the mean velocity, which are then used in the computation of turbulence intensity. The Box–Jenkins procedure was applied to the water velocity data collected at each horizontal position and at each of the eight elevations above the bottom for each replicate seagrass bed. However, because of the time constant limitation of the Marsh-McBirney flow meter, the measurement of $U_{\mathrm{rms}}$ did not include fluctuations in current velocity at frequencies greater than 5 Hz.

The mean $U_{\mathrm{rms}}$ for each horizontal position was calculated for each replicate shoot arrangement exposed to each flow treatment. For unidirectional flow, at each horizontal position, $U_{\mathrm{rms}}$ was averaged for all the heights within the deflected canopy to yield the mean $U_{\mathrm{rms}}$ within the canopy. Turbulence intensity was also averaged over all the heights above the canopy to yield the mean $U_{\mathrm{rms}}$ over the canopy. In contrast, mean $U_{\mathrm{rms}}$ for the oscillatory flow treatments was calculated using $U_{\mathrm{rms}}$ from all eight elevations because the blades swept back and forth through all the elevations. As for unidirectional flow, turbulence intensity arising from oscillatory flow trials was examined under three-way ANOVA for effects above and within the canopy, with main effects of downstream distance, flow regime and shoot arrangement.

### 2.10. *Effects of arrangement on force experienced by shoots*

Force transducers were mounted at the same three horizontal positions within the test section at which velocity profiles were recorded. The transducers were mounted such that the sting extended up through a hole (25 mm in diameter) in the clear acrylic plate that held the seagrass shoots; the sting protruded 5 mm above the surface of the plate (Fig. 3). The shoots attached to the force transducers were arbitrarily chosen from the 170 shoots collected for each replicate experimental canopy. A shoot was cut from the rhizome just below the first visible root node (observed location of failure; author's unpublished data) and attached to a piece of aluminum rod (1 cm long) by a band of aluminum duct tape 5 mm wide. The aluminum rod fit snugly over the sting of the force transducer. Shoots were oriented as observed in nature with their blade width at 90° to the flow direction. Flow-induced force was recorded from each transducer for 250 s at 50 Hz for each of the flow treatments described above. Voltage signals from the force transducers were processed using a Vishay Strain Indicator (Model #p-3500) and recorded using the data acquisition system described above. For unidirectional flow, mean drag force on a shoot was computed for each position within the test section. For oscillatory flow, the mean of the absolute values of the maximum flow-induced forces was calculated.

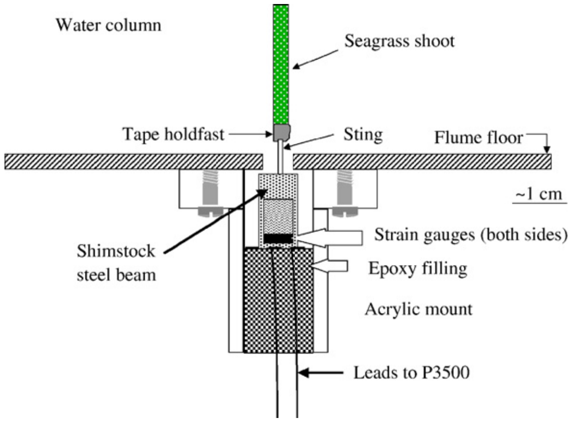

Fig. 3. Force transducer design. P3500 refers to the Vishay strain meter in a half bridge configuration. For presentation purposes and to show the strain gauge position, the force transducer is shown rotated at a 90° angle to its actual alignment in the flume relative to the direction of flow.

After a replicate experimental canopy had been subjected to all flow treatments, the shoots attached to a force transducer were cut from their aluminum tape hold fasts, leaving the tape in place on the sting. All flow treatments were repeated and the flow-induced force on the sting plus attached tape was recorded for each force transducer, for each flow treatment. In unidirectional flow, the mean drag force for each position and each flow treatment was calculated for the sting and tape alone. This value was subtracted from the mean drag force calculated with the shoot attached to yield the force on the shoot alone, for each position and flow treatment. Likewise, under oscillatory flow, the mean of the absolute values of maximum flow-induced forces on the sting and tape alone was subtracted. For both the unidirectional and oscillatory flow trials, flow-induced force was compared (after natural log+1 transformation) under three-way ANOVA for effects above and within the canopy, with main effects of downstream distance, flow regime and shoot arrangement.

### 2.11. *Drag vs. Reynolds number*

We plotted drag as a function of Reynolds Number in order to compare all the combinations of flow and arrangements. The drag coefficient ($C_{\mathrm{d}}$) is a non-dimensional coefficient that indicates how drag-inducing the shape of a body is. For seagrass shoots in unidirectional flow, we calculated $C_{\mathrm{d}}$ using the equations (Vogel 1994):

$$C_{\mathrm{d}} = (2F)/(\delta S U^2) \tag{4}$$

where: $F$ is the drag force on the shoot, $S$ is the observed canopy height (location of blade tips; canopy height was measured on video images of the canopy during each combination of flow velocity and plant arrangement), and $U$ is the flow velocity. For each unidirectional flow treatment, we used the arithmetic mean of the mean time-averaged velocities of all the within-canopy elevations at a horizontal position as U to calculate $C_{\mathrm{d}}$.

Table 1
Summary statistics of seagrass shoot morphology

| Plant component | Length (m) | Width (m) | Two-dimensional surface area ($m^2$) | Cross-sectional area ($m^2$) |
|---|---|---|---|---|
| Whole plant | 0.21 [0.056] | | 0.002 [0.0008] | |
| Blades | 0.15 [0.044] | 0.003 [0.0005] | | $3.221\times10^{-7}$ [$1.479\times10^{-7}$] |
| Sheathes | 0.05 [0.013] | 0.003 [0.0005] | | $4.835\times10^{-6}$ [$1.673\times10^{-6}$] |

Values in [ ] are one standard deviation.

We calculated the Reynolds Number ($Re_s$) of each shoot for which we measured drag in unidirectional flow, where:

$$Re_s = U_s L_s / v \tag{5}$$

where $U_s$ is the arithmetic mean of the mean time-averaged velocities (m $s^{-1}$) measured at each elevation within the canopy at the horizontal position within the tank where the shoot was placed, $L_s$ is the length of the shoot, and $v$ is the kinematic viscosity of seawater at 20 °C ($1.047\times10^{-6}$ $m^2$ $s^{-1}$) (see Eq. (2)).

### 2.12. Environmental Stress Factor (ESF)

This factor is the ratio of the strength (force per cross-sectional area required to break the material) of a tissue to the maximum stress (force per cross-sectional area) it experiences in its day-to-day existence in its natural habitat at that stage in its life (*sensu* Johnson and Koehl, 1994). In the case of seagrass blades, which are put under load by waves and currents, the tensile strength in a blade is the force on the blade divided by the blade's cross-sectional area; thus, ESF can be simplified to the force required to break a blade divided by the day-to-day hydrodynamic force experienced by that blade at that stage in its life.

The force to break a blade was measured with a hand-held force transducer (precision = 0.001 N) (Kopp, 1999), by wrapping the second oldest leaf around a capstan-like grip and manually pulling the leaf for 1–2 s (a rate chosen to be comparable with the wave periods used in the flume study) until failure (as described by Kopp, 1999). *Z. marina* typically has three to four leaf blades, with new blades being formed approximately every two weeks throughout the year, with the youngest leaf typically not fully emerged from the sheath and the oldest leaves being necrotic and heavily epiphytized. The second oldest leaf was chosen because it has been shown to be the part of the seagrass plant in which the maximum photosynthetic rate occurs (Thayer et al., 1984). Thus, damage to or loss of this second oldest leaf could have severe physiological impact on the plant. Whole plants were gripped at the rhizome and the second oldest leaf pulled at a 45° angle in an attempt to mimic the direction in which we have observed seagrass plants to be pulled by currents under field flow conditions. Blades failed at the narrow constriction that forms where the blades emerge from the sheath.

Maximum force to break the second oldest leaf was measured on 590 plants, 250 collected in August 1996, and 340 collected in June, 1997. These dates were chosen in order to capture any seasonal variation in tissue strength that may have occurred between the post- and pre-summer heat stress, respectively, for *Z. marina* near Beaufort (Thayer et al., 1984). During these times of year, very similar flow conditions exist in the field in terms of tidal currents and wind waves (dominant SW winds of ~15 kph), meaning that the flume settings to which plants were exposed reflect relatively high energy conditions. Plants were collected from the same field locations as used for the flow and light experiments. The areas surrounding these sites were also surveyed over the same time period by Fonseca and Cahalan (1992) for wave conditions and by Fonseca and Bell (1998) for tidal current velocities. Flow data from these two studies were used to determine the unidirectional current velocities and the wave conditions used in the flume experiments described above were used to set the experimental conditions in the flume, providing the context for computation of ESF, which requires matching physical conditions at these sites over the same seasons with the condition of the plants during those seasons when breaking strength was tested. During these times (June and August), tidal current velocities are lower than early spring and late fall when the amplitude of the astronomical tides are of greater amplitude. Similarly, wind conditions are dominated by gentle southwesterly flows, and do not often exceed average annual conditions (Fonseca and Bell, 1998). Thus, the current and wave conditions used here represent conditions that are to the high side of what the plants may experience day-to-day, at these sites and over these seasons. One-way ANOVA was used to compare the differences among force at tissue failure among seasons (after natural log + 1 transformation).

Following Johnson and Koehl (1994), ESF was computed in order to gauge the potential susceptibility of the plants to breakage and ultimately, the relative importance of any difference in flow-induced force experienced as the result of shoot arrangement. ESF is the ratio of the strength ($\sigma_{\text{breaking}}$; the stress required to break

Table 2
Three-way ANOVA of force (Newtons) on seagrass shoots by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed)

| Source | *d.f.* | F | Pr>*F* |
|---|---|---|---|
| Position (*P*) | 2 | 0.11 | 0.8969 |
| Arrangement (*A*) | 1 | 3.08 | ***0.0925*** |
| Flow (*F*) | 1 | 7.76 | ***0.0103*** |
| *P*F* | 2 | 0.01 | 0.9947 |
| *A*F* | 1 | 0.45 | 0.5067 |
| *P*A* | 2 | 0.68 | 0.5141 |
| *P*A*F* | 2 | 0.21 | 0.8099 |

Bold and italicized values denote important trends.

the tissue $=F_r/A_o$; where $F_r$ = the force with which the specimen resists extension and $A_o$ = cross-sectional area at time 0, before stress is applied) of a component of an organism at some stage in its life (in this case, the second oldest blade of a non-flowering plant in its first year of life) to the typical maximum stress ($\sigma_{\text{drag}}$; where the force is the flow-induced force as measured by the force transducer and $A_o$ is as defined above) experienced by that component as it is used day-to-day in the habitat of the organism during that life stage (in this case, the stress in the blade due to the average flow-induced force on the blade during unidirectional and oscillatory flow treatments in the flume) (Johnson and Koehl, 1994). In contrast, the safety factor of a component of an organism is the ratio of the strength of the tissue from which the component is made to the peak stress that it experiences during its lifetime (Alexander, 1981). Although unidirectional flow velocities used in this study cover the range of conditions (and thus, flow-induced force) that the plants typically experience on a day-to-day basis near Beaufort, NC (Fonseca and Bell, 1998), flow-induced forces that might be experienced under aperiodic storm events are not represented by the flume conditions. Because ESF values were computed based on maximum flow-induced forces observed under both unidirectional and oscillatory flow in the flume, the ESF value for oscillatory flow will likely be an overestimate.

Table 3
Means of force on individual shoots under unidirectional flow by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed)

| Position | N | Mean |
|---|---|---|
| 0 | 12 | 0.024 |
| 50 | 12 | 0.026 |
| 100 | 12 | 0.021 |
| Arrangement | N | Mean |
| Random | 18 | 0.031 |
| Row | 18 | 0.017 |
| Flow | N | Mean |
| Low | 18 | 0.013 |
| High | 18 | 0.035 |

Units are in Newtons.

### 2.13. Effects of shoot arrangements on light interception by the canopy

The effect of shoot arrangement on light interception by the canopy was assessed for each of the flow conditions described above. Photon flux densities of photosynthetically active radiation (PAR) were measured using a Li-Cor $2\pi$ sensor (a flat plate sensor that is sensitive to the angle of incidence of light as it impinges on the sensor). The sensor was attached to an armature that allowed manipulation of the position of the sensor underneath the acrylic plate of the test section. The flat surface of the sensor was pressed up against the plate between shoots at ten points along the length of the midline of the plate. These points were evenly spaced at 0.09 m intervals along the length of the plate for shoots in rows, but had to be shifted slightly in the random shoot arrangements to assure that the probe did not end up directly under a shoot. The halogen flood light described above for the EI and buoyancy tests was used as the light source. It was positioned 0.6 m above the

Table 4
Three-way ANOVA of turbulence intensity within and above the seagrass canopy by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed)

| Source | *d.f.* | F | Pr>*F* |
|---|---|---|---|
| *Within the canopy* | | | |
| Position (*P*) | 3 | 10.95 | ***0.0001*** |
| Arrangement (*A*) | 1 | 3.41 | ***0.0681*** |
| Flow (*F*) | 1 | 11.90 | ***0.0009*** |
| *P*F* | 3 | 0.32 | 0.8123 |
| *A*F* | 1 | 0.41 | 0.5239 |
| *P*A* | 3 | 0.34 | 0.7943 |
| *P*A*F* | 3 | 0.39 | 0.7589 |
| *Above the canopy* | | | |
| Position (*P*) | 3 | 2.69 | ***0.0472*** |
| Arrangement (*A*) | 1 | 31.51 | ***0.0001*** |
| Flow (*F*) | 1 | 112.59 | ***0.0001*** |
| *P*F* | 3 | 2.46 | ***0.0641*** |
| *A*F* | 1 | 0.45 | 0.5022 |
| *P*A* | 3 | 1.48 | 0.2204 |
| *P*A*F* | 3 | 0.27 | 0.8490 |

Bold and italicized values denote important trends.

Table 5
Means of turbulence intensity measures by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed) within and above the canopy

| Within the canopy | | |
|---|---|---|
| *Position* | N | Mean |
| −25 | 25 | 18.85 |
| 0 | 15 | 19.33 |
| 50 | 15 | 29.98 |
| 100 | 15 | 34.43 |
| *Arrangement* | N | Mean |
| Random | 40 | 22.98 |
| Row | 60 | 27.42 |
| *Flow* | N | Mean |
| Low | 40 | 28.96 |
| High | 60 | 20.67 |

| Above the canopy | | |
|---|---|---|
| *Position* | N | Mean |
| −25 | 55 | 18.24 |
| 0 | 54 | 18.85 |
| 50 | 55 | 21.16 |
| 100 | 54 | 20.16 |
| *Arrangement* | N | Mean |
| Random | 88 | 16.87 |
| Row | 130 | 21.45 |
| *Flow* | N | Mean |
| Low | 98 | 24.29 |
| High | 120 | 15.78 |

Units are in m $s^{-1}$.

flume bottom (0.35 m above the water surface) directly over the sensor, thus, the light was moved each time the sensor was moved. The output of the Li-Cor sensor was recorded for 30 s (sampling rate = 50 Hz) at each point along the tank with the system described above for flow and force.

Photon flux density when no shoots were present was also measured for each flow treatment at each point along the tank, as described above. Percent light transmission through the canopy at a point along the length of the plate was calculated by dividing the light transmitted through the canopy by the light transmitted when no shoots were there and multiplying by 100. For each replicate shoot arrangement under each flow treatment, the mean of the percent light transmission at the ten points along the plate was calculated. Average percent light transmission was arcsine-transformed before statistical analysis and was compared among shoot arrangements for each flow treatment using one-way ANOVA and Tukey's test.

## 3. Results

### 3.1. Seagrass morphology- individual shoots and canopy height

Plants used in these experiments are described in Table 1. Overall plant length was nearly equal to water depth (0.21 m mean length vs. 0.25 m water depth). Based on measurements taken from photographs, the range of canopy heights for each flow treatment was determined. Under no flow, still water canopy height ranged from 10.1–12.7 cm. Under the 0.30 m $s^{-1}$ flow treatment, canopy height ranged from 9.4–11.0 cm, approximately 90% of still water canopy height. Under the 0.55 m $s^{-1}$ flow treatment, canopy height ranged from 6.5–7.2 cm, approximately 60% of still water height.

### 3.2. Calibrations—plant flexural stiffness and buoyancy

The flexural stiffness (EI) of blades and sheaths of individual *Z. marina* plants exposed for 48 h to saturating light were not significantly different from plants kept in darkness for 48 h ($p > 0.05$). Sheath EI (mean = $1.77 \times 10^{-7}$, s.d. = $1.000 \times 10^{-7}$) were roughly twice as stiff as leaves (mean = $7.998 \times 10^{-8}$, s.d. = $2.462 \times 10^{-7}$).

In the buoyancy tests, all plants, whether kept in light or dark, remained positively buoyant after 48 h. The buoyancy of individual *Z. marina* plants exposed for 48 h to saturating light were not significantly different

Table 6
Three-way ANOVA of mean profile velocity within and above the seagrass canopy by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed)

| Source | *d.f.* | F | Pr > *F* |
|---|---|---|---|
| *Within the canopy* | | | |
| Position (*P*) | 3 | 0.44 | 0.7238 |
| Arrangement (*A*) | 1 | 6.39 | ***0.0133*** |
| Flow (*F*) | 1 | 14.56 | ***0.0003*** |
| *P*F* | 3 | 0.08 | 0.9683 |
| *A*F* | 1 | 0.35 | 0.5550 |
| *P*A* | 3 | 0.43 | 0.7352 |
| *P*A*F* | 3 | 0.29 | 0.8315 |
| *Above the canopy* | | | |
| Position (*P*) | 3 | 1.02 | 0.3856 |
| Arrangement (*A*) | 1 | 20.54 | ***0.0001*** |
| Flow (*F*) | 1 | 55.25 | ***0.0001*** |
| *P*F* | 3 | 0.97 | 0.4077 |
| *A*F* | 1 | 0.67 | 0.4142 |
| *P*A* | 3 | 0.54 | 0.6527 |
| *P*A*F* | 3 | 0.12 | 0.9494 |

Bold and italicized values denote important trends.

Table 7
Means of current velocity by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed) within and above the canopy

| *Within the canopy* | | |
|---|---|---|
| Position | N | Mean |
| −25 | 25 | 0.40 |
| 0 | 25 | 0.41 |
| 50 | 27 | 0.38 |
| 100 | 27 | 0.35 |
| Arrangement | N | Mean |
| Random | 40 | 0.46 |
| Row | 64 | 0.34 |
| Flow | N | Mean |
| Low | 62 | 0.32 |
| High | 42 | 0.49 |
| *Above the canopy* | | |
| Position | N | Mean |
| −25 | 55 | 0.44 |
| 0 | 54 | 0.48 |
| 50 | 55 | 0.51 |
| 100 | 54 | 0.46 |
| Arrangement | N | Mean |
| Random | 88 | 0.55 |
| Row | 130 | 0.41 |
| Flow | N | Mean |
| Low | 98 | 0.35 |
| High | 120 | 0.57 |

Units are in $ms^{-1}$.

from those of plants kept in darkness for 48 h (one-way ANOVA; $p>0.40$, $n=15$). Buoyancy averaged $2.32\times10^{-6}$ N mm$^{-3}$, s.d.$=7.65\times10^{-7}$ N mm$^{-3}$.

### 3.3. Unidirectional flow trials

There were no significant interaction effects of downstream distance, shoot arrangement and flow on force experienced by shoots ($P>0.05$). Force on individual shoots did not change significantly with position, but did as a function of both shoot arrangement and flow velocity (Table 2). Shoots arranged randomly experienced ~twice the force of shoots arranged in rows (Table 3). Shoots under the high flow conditions (average in-canopy of current=0.32 $ms^{-1}$ for low, 0.49 for high) experienced ~three times the force of shoots under low flow.

For measures of turbulence intensity *within* the canopy, there were no significant interaction effects (Table 4). All three main effects were either significant at $p<0.05$ or nearly so. $U_{rms}$ increased with downstream distance and was slightly higher for low flow than high flow (Table 5). Shoots arranged in rows tended to produce a higher $U_{rms}$ than those arranged randomly. For $U_{rms}$ *over* the canopy, there was a significant interaction of position and flow (Table 4). There was a significant effect of shoot arrangement with $U_{rms}$ *over* the canopy being higher for plants arranged in rows, than those arranged randomly.

There were no significant interaction effects of downstream distance, shoot arrangement and flow on mean profile velocity both *within* and *above* the canopy (Table 6). *Within* the canopy, mean profile velocity decreased with downstream position. Shoots arranged randomly allowed for a higher mean profile velocity than those arranged in rows (Table 7). *Above* the canopy, current speed showed an initial increased upon entering the canopy area and again, shoots arranged randomly allowed for a higher mean profile velocity than those arranged in rows. Similarly, for percent change in velocity, there were no significant interaction terms (Table 8). Position, arrangement and flow all had significant effects *within* the canopy, whereas only arrangement had a significant effect *above* the canopy (Table 9). Shoots arranged randomly had less of an effect on percent velocity reduction. Increased downstream position increased the percent flow reduction and, unsurprisingly, the higher flow speed allowed for less of a reduction in current velocity through the canopy than the lower ambient flow speed.

### 3.4. Unidirectional flow— $C_d$ & $Re_s$ relationship

The drag coefficients ($C_d$) of plants in unidirectional flow are plotted as a function of shoot Reynold's Number ($Re_s$) (Fig. 4). Over the lower range of $Re_s$ values (0 to ~75,000) shoots in random arrangements

Table 8
Three-way ANOVA of percent velocity reduction within and above the seagrass canopy by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed)

| Source | *d.f.* | F | Pr>*F* |
|---|---|---|---|
| *Within the canopy* | | | |
| Position (*P*) | 2 | 13.78 | ***0.0001*** |
| Arrangement (*A*) | 1 | 4.91 | ***0.0364*** |
| Flow (*F*) | 1 | 12.36 | ***0.0018*** |
| *P*F* | 2 | 0.29 | 0.7474 |
| *A*F* | 1 | 0.03 | 0.8682 |
| *P*A* | 2 | 0.82 | 0.4531 |
| *P*A*F* | 2 | 1.47 | 0.2510 |
| *Above the canopy* | | | |
| Position (*P*) | 2 | 0.44 | 0.6512 |
| Arrangement (*A*) | 1 | 4.55 | ***0.0434*** |
| Flow (*F*) | 1 | 0.29 | 0.5959 |
| *P*F* | 2 | 0.91 | 0.4166 |
| *A*F* | 1 | 0.11 | 0.7453 |
| *P*A* | 2 | 0.15 | 0.8577 |
| *P*A*F* | 2 | 0.67 | 0.5201 |

Bold and italicized values denote important trends.

Table 9
Means of percent current velocity reduction by downstream distance (position), shoot arrangement (rows, random) and flow (low, high unidirectional current speed) WITHIN and ABOVE the canopy

| *Within the canopy* | | |
|---|---|---|
| Position | N | Mean |
| 0 | 12 | −10.1 |
| 50 | 12 | −20.8 |
| 100 | 12 | −30.7 |
| Arrangement | N | Mean |
| Random | 18 | −17.0 |
| Row | 18 | −24.1 |
| Flow | N | Mean |
| Low | 18 | −26.2 |
| High | 18 | −14.9 |
| *Above the canopy* | | |
| Position | N | Mean |
| 0 | 12 | −12.4 |
| 50 | 12 | −10.7 |
| 100 | 12 | −16.6 |
| Arrangement | N | Mean |
| Random | 18 | −7.6 |
| Row | 18 | −18.9 |
| Flow | N | Mean |
| Low | 18 | −11.8 |
| High | 18 | −14.7 |

Units are percent as compared with upstream values.

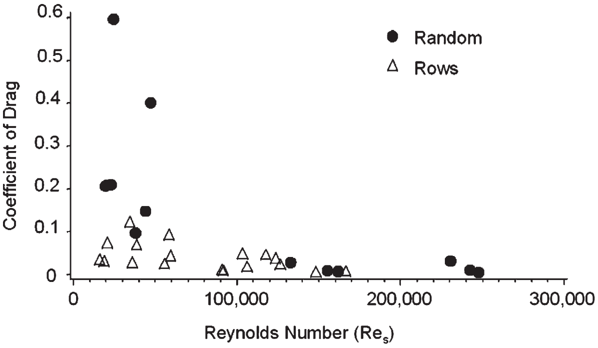

Fig. 4. Plot of coefficient of drag ($C_d$) vs Reynolds number ($Re_s$) for all flow treatments. Dots represent treatments with shoots in random arrangements; triangles represent treatments with shoots in rows.

exhibited higher drag coefficients. However, at $Re_s >$ 100,000, seagrass shoot arrangement had no effect on $C_d$ (consistent with the somewhat weak significance detected for arrangement effects in low flow treatments under the three-way ANOVA).

### 3.5. Oscillatory flow trials

Tests for differences in velocity and $U_{rms}$ under control trials found no significant difference among positions within the test section ($p \gg 0.05$; not shown). Like current velocity reduction under the unidirectional flow treatments, three-way ANOVA (not shown) found no significant interaction effect among shoot arrangement and position on current velocity for either wave treatment. There was also no effect of shoot arrangement on current velocity *within* the seagrass canopy, irrespective of the wave treatments. Position effect was weakly significant ($p < 0.07$), but only under the shorter period wave treatment. At 0.05 and 0.5 m into the test section, mean maximum water velocity ranged between 14.5 and 15 cm s$^{-1}$, but dropped to 7.5 cm s$^{-1}$ by 0.95 m into the test section.

Turbulence intensity was higher under oscillatory flow than under unidirectional flow. The effect of shoot arrangement and downstream position on turbulence intensity ($U_{rms}$) was also examined under two-way ANOVA (not shown). There was no significant interaction among the main effects, and no significant main effects ($p > 0.05$). For the treatment with shorter wave period there was a tendency for $U_{rms}$ to decrease with distance from the paddle wave generator (near 100% at 0.05 m into the test section, and dropping to 41% by 0.5 m and 16% by 0.95 m. However, due to large variation, these differences were not significant ($p > 0.05$). Under the longer treatment with longer wave period, there was no such tendency for decreasing $U_{rms}$ and values ranged between 78% and 92%.

The effect of shoot arrangement and downstream position on flow-induced force experienced by individual shoots was examined under three-way ANOVA (not shown). There was no significant interaction effect among position, wave type and shoot arrangement. There was also no significant effect of shoot arrangement on flow-induced force experienced by the individual shoots. Overall there was a significant effect of horizontal distance on flow-induced force ($p < 0.05$) with force on shoots. Shoots at the position nearest the wave generator experienced the highest force, but that force had dropped

Table 10
Means of force on individual shoots under oscillatory flow by downstream distance (position), shoot arrangement (rows, random) and wave setting

| Position | N | Mean |
|---|---|---|
| 100 | 10 | 0.046 |
| 50 | 10 | 0.073 |
| 0 | 10 | 0.098 |
| | | |
| Arrangement | N | Mean |
| Random | 18 | 0.070 |
| Row | 12 | 0.075 |
| Wave period (s) | N | Mean |
| 2.0 | 15 | 0.035 |
| 2.6 | 15 | 0.110 |

Units are in Newtons. Period is in seconds (s).

Table 11
Effect of shoot arrangement (row vs. random) on light attenuation under unidirectional flow and waves

| | Arrangement | Percent light attenuation | % Difference in attenuation |
|---|---|---|---|
| *U (m s$^{-1}$)* | | | |
| 0.30 | Random | −15.6 | 34.7** |
| | Row | −23.9 | |
| 0.55 | Random | −23.6 | 11.0 |
| | Row | −26.5 | |
| *Wave period (s)* | | | |
| 2.25 | Random | −16.6 | 23.5 |
| | Row | −21.7 | |
| 2.50 | Random | −14.5 | 25.6 |
| | Row | −19.5 | |

$U$=velocity; (N)=force in Newtons. **=significantly different at $P>F=0.05$ (ln+1 transformed values used to compute Pr>$F$). % Difference=([greater/lesser]−1) *100.

50% by 1 m (Table 10). The wave treatment with the longer wavelength produced nearly three times the force on shoots than the short wavelength treatment.

### 3.6. Environmental Stress Factor (ESF) of plants

Peak force at tissue failure was not significantly different ($p>0.05$) among the June and August samples and values were pooled. For unidirectional flow, the highest drag force value was 0.033 N, while under oscillatory flow, the highest flow-induced force value was 0.149 N— approximately 4.5 times greater than under the high (unidirectional) flow treatment. Using the cross-sectional area of a single blade, the ESF value calculated for unidirectional flow was 41.88 while under oscillatory flow, the ESF value was 9.28.

### 3.7. Canopy light interception

Under both oscillatory and unidirectional flow conditions, shoots arranged in rows consistently reduced light transmission to the artificial sea floor by about 24% (Table 11). However, a statistically significant difference among shoot arrangement treatments was only found under the low flow treatment (Tukey's test: $p<0.05$) with plants in rows intercepting more light.

## 4. Discussion

The interaction of water motion and the seagrass canopy conformed to the findings of previous studies; under unidirectional flow, current velocity increased over the canopy with downstream distance while decreasing both within the canopy and downstream distance (Fonseca et al., 1982, 1983; Fonseca and Fisher, 1986; Eckman, 1987; Gambi et al., 1990; Abdelrhman, 2003). The seagrass canopy compressed with increased water current velocity (although ∼25% less than predicted by Fonseca and Kenworthy (1987)) and turbulence intensity ($U_{\mathrm{rms}}$) increased both within the canopy and generally with downstream distance, as seen by Gambi et al. (1990), Abdelrhman (2003) and suggested by Ackerman and Okubo (1993). The patterns of flow reduction for this canopy scale (length and width) are consistent with that described by Fonseca and Koehl (2006) for the effects of patch width. Changes in $U_{\mathrm{rms}}$ of the flow field are also well-documented phenomena, not only for flow in and around seagrass canopies (Ackerman and Okubo, 1993; Koch, 1993; Verduin, 1997), but for marine algae as well (Anderson and Charters, 1982; Koehl and Alberte, 1988). Studies of seagrass–flow interactions all converge on common general tendencies of flow velocity reduction and enhanced turbulence intensity, all with distance into the canopy, for both unidirectional and oscillatory flow.

Previous studies have demonstrated reduction of wave height as they pass through seagrass canopies (Fonseca and Cahalan, 1992; Wallace and Cox, 1997). Here, as for the previous studies, wave-induced force on shoots was attenuated with horizontal distance into the bed, but only for the waves of shorter period. Flow velocities through the canopy for the wave treatments with longer wave period, which also had greater wave height, were not significantly diminished by the test section, which was only 1 m long. A diminishing effect of wave height reduction with increased wave height and period was also found by Fonseca and Cahalan (1992) and Knutson et al. (1982) for marsh studies. Also, turbulence intensity increased with distance into the canopy, which logically signals reduction in wave energy through the canopy.

The direct measurements of drag force (via force transducers) on individual shoots may be the first reported for seagrasses and support observations from previous studies regarding drag generated by the canopy on the passing flow (Fonseca et al., 1982; Gambi et al., 1990). Shoots arranged randomly under unidirectional flow, as well as under the wave treatments with longer period experienced greater flow-induced force, higher profile velocities but lower turbulence intensity than shoots arranged in rows (albeit non-significantly with waves). Conversely, plants arranged in rows experienced lower force, slightly higher turbulence intensity, but engendered lower mean profile velocities within the canopy, suggesting better streamlining; deflection of flow over and around the test section, as seen for other flexible biota (Charters et al., 1969; Koehl, 1976, 1977, 1986; Denny et al., 1985; Denny, 1988; Koehl and Alberte, 1988; Carrington, 1990).

The lower force experienced by shoots arranged in rows when viewed under the lower in-canopy flow and higher turbulence intensity, suggests a series of trade-offs (see summary; Table 12). As has been pointed out in many previous studies, the collapse of the canopy and higher velocity over the canopy (with concomitant reduction of in-canopy velocity) results in protection of the erodable sediment surface by transferring force to the canopy. Interestingly, the force data reveal fairly constant force on shoots within either arrangement, irrespective of distance into the test section. This constancy in force reveals the complimentary effects of high bending at the meadow edge (presenting a smaller frontal area to the flow where velocity is higher) and lessened bending deeper into the meadow – with correspondingly higher frontal area– as velocity is reduced (*sensu* Fonseca and Kenworthy, 1987). To our knowledge, this may be the first time that this specific role of seagrass shoot flexibility (effect of frontal area change with flow velocity) has been demonstrated in a quantitative manner. Such an equal distribution of force reduces the accumulation of force on individual shoots at meadow edges, which could otherwise disrupt the ability of the plants to spread vegetatively. Previous to commencing this study, there were apparently little or no data on forces acting on clonally integrated plants (K. Niklas, Cornell Univ., pers. com. 1994). Thus, the shoot arrangement with both the lowest $C_d$ across the range of $Re_b$ (here, rows) may be the arrangement most likely to produce the greater community stability (*sensu* Fonseca and Fisher, 1986). We speculate that the difference in $C_d$ may have been sustained across a greater range of $Re_s$ and $U$ if we had tried different row spacing (our selection may have been sub-optimal).

Nonetheless, with the row arrangement chosen for this study, we were unable to detect any ecological benefit for seagrass shoots to arrange in rows under conditions of oscillatory flow. As we speculated for rows, we again may not have struck upon the optimum arrangement for these oscillatory flow conditions that would have yielded a significant spacing effect. We posit that when highly flexible plants such as seagrasses are subjected to oscillatory flow (as opposed to unidirectional flow where canopy movement is far less), that there may be a different specific tuning of spacing to chronic wave conditions, inherent blade flexibility and fouling, etc. Studies that measure force on shoots under varied spacing shoot morphology and flexibility under oscillatory flow would possibly identify the appropriate balance of conditions leading to row formation. Such fine scale manipulation may be needed based on recent findings from coastal engineering studies. Duclos and Clement (2004) found that even small levels of disorder among inflexible vertical cylinders were shown to dramatically disrupt force buildup on individual cylinders. We speculate that similarly small changes in element spacing may also be important for the highly complicated scenario of highly flexible elements (seagrass), with concomitantly dramatic benefits for individual element stability; this remains an area ripe for investigation.

We also asked whether light interception by the canopy varied with shoot arrangement and if this could be a selection factor in driving arrangement. However, at no time did shoots arranged in rows intercept less light than those arranged randomly (Table 11). There was a tendency for shoots arranged in rows to intercept more light than those arranged randomly, under the low unidirectional flow treatment. Although bending of the canopy has been shown to increase mutual shading among the seagrass shoots (Dennison, 1979; Short, 1980) as compared to when the shoots were upright, the reduction in light passing through the canopy means that the shoots intercepted more light as a group than when they were more upright. However, we cannot speculate as to the physiological feedback mechanism that could produce the apparent self-organization described here.

As shoots were swept back and forth under oscillatory flow, more light passed through the canopy than under

Table 12
Summary of relationship among dependent and independent variables for unidirectional flow

| | Force | $U_{rms}$ | | Mean profile velocity | | Percent velocity reduction | |
|---|---|---|---|---|---|---|---|
| | | Within | Above | Within | Above | Within | Above |
| Arrangement (ran) | + | – | – | + | + | – | – |
| Arrangement (row) | – | + | + | – | – | + | + |
| Flow (low to high) | + | – | – | + | + | – | – |
| Position (downstream) | ∅ | + | + | ∅ | ∅ | + | ∅ |

Pluses indicate either which in a pair of comparisons was larger for a given independent variable (comparisons of arrangements) or whether the trend was positive, negative or neutral (comparisons of flow and position).

unidirectional flow (Table 11). Shoot waving may have the added benefit of allowing light to reach more of a plant's photosynthetic units than might occur when the canopy is compressed under unidirectional flow (*sensu* Koehl and Alberte, 1988). Direct measurements of seagrass physiological responses and light interception under different flow conditions are needed to determine any trade-offs to plant growth as the result of movement and light capture ability.

Even though differences in flow-induced force, $U_{\mathrm{rms}}$ and light capture were detected among shoot arrangement treatments, there was no obvious trade-off between flow-induced force and light capture that might plausibly act as a trigger for different shoot arrangements. Even though the differences in light capture among shoot arrangements were sometimes slight, over time even small differences in light capture ability, if consistently realized, may translate into a measurable ecological benefit to the plants (and perhaps more so at a better tuned spacing). Increased light interception by the canopy, especially under low flow conditions (Table 11) should provide the ecological benefit of increased photosynthesis and potentially, asexual and/or sexual reproduction.

Yet, at this point, we may only suggest that water motion, as opposed to light capture, is the dominant physical mechanism responsible for these shoot arrangements. Again, the tests conducted here utilized only one row spacing configuration that we interpolated from other observed field configurations and the results may not represent the optimum spacing that would have arisen had the beds been grown under the various flow conditions. The spacing used in the flume experiments was based on a coarse sampling of a wide variety of flow regimes and highly variable plant morphologies (Fig. 1). From the small photographic sample size, the ratio of shoot length/row spacing ranged tremendously (0 to 500% overlap) and for *Z. marina* had only one observation of row overlap, and no clear *a priori* relationship of row spacing to flow conditions could be hypothesized. Additional survey work documenting the conditions under which row spacing occurs to better define the association of shoot organization with flow conditions.

It has been shown here that row arrangement can result in reduced flow-induced force on individual shoots and potential photosynthetic benefit, but these experiments do not demonstrate how a seagrass clone, spreading across the sea floor, would interact with the flow to produce a row pattern. Anecdotal evidence from *Posidonia coriacea* suggests that row formations perpendicular to the flow axis extend only across the margins of larger patches (Fig. 1). Row formation may be lost as patches grow because of a loss of a strong uniaxial flow signal (*sensu* Ackerman and Okubo, 1993), as hinted by the increase in turbulence intensity over downstream distance into the canopy. However, if growth tends in rows throughout the patch or even at the margins, we would expect that the net effect would be a greater spread across the flow direction than with the flow, and some landscape scale survey work supports this idea (Fonseca, 1996). Finer scale examinations, including measurement of the influence of shoot orientation to the flow on flow-induced force experienced by the shoot is required.

We also asked whether arrangement might affect the Environmental Stress Factor (ESF). Irrespective of shoot arrangement, the Environmental Stress Factor (ESF) ranged between ~50 for unidirectional flow and ~10 for oscillatory flow, the latter being within the same range of values found by Johnson and Koehl (1994) for kelp. The data were insufficient to determine whether the site-relevant, *Z. marina* ESF would change among seasons and flow conditions as it does for kelp (*Nereocystis luetkeana*). Johnson and Koehl (1994) found that ESF was maintained by *N. luetkeana* between sites and during seasons as plants grew and flow conditions changed. However, besides canopy streamlining through deflection, row-induced reduction in flow-induced force, may help maintain an ESF conducive to offsetting damage to the critically important, photosynthetically active blades.

The ESF value for treatments under waves was approximately four and a half times closer to tissue failure than under the highest unidirectional flow used here, and provides strong evidence that much larger, storm-induced waves (i.e., extreme events, Gaines and Denny, 1993) provide the greatest potential for mechanical damage to seagrass shoots. Unlike unidirectional flow when the canopy is deflected into a hydrodynamically smooth shape, waves sweep the canopy back and forth, and when wave lengths are sufficiently long, seagrass shoots will be pulled to full extension and experience flow-induced forces much greater than that of unidirectional flow (much as described for kelp stands, Koehl, 1986). Older blades on the shoot that are often partially necrotic likely dehisce first, before the younger, more photosynthetically productive and probably stronger blades are damaged (this theorized absence of older, necrotic and more heavily epiphytized blades may also support the observation that seagrass beds in current-swept areas appear greener and "healthier"; *sensu* Conover, 1964). Results of Patterson et al. (2001) also suggest that there is significant variation among reproductive shoot strength and that this could be a selective factor for flowering shoots during extreme events. A similar comparison for vegetative shoots remains to be undertaken. Under the most extreme conditions, it may be possible for the entire above-ground shoot to break off at the small constriction occurring at the base of the sheath.

Although seagrass beds are known to be uprooted during storms primarily as the result of sediment erosion from under the root-rhizome complex at the edge of patches (Fonseca et al. 2000), the ESF data given here indicate that damage to seagrass beds may also occur as the result of blade breakage. The possibility of a synergistic effect between shoot damage, loss of canopy structures (allowing more wave energy to be transferred to the sediment surface) and erosion events require additional investigation.

Are there alternative sources of seagrass shoot arrangement? The spread of seagrass across the sea floor is, of course, mediated by many other factors, acting across larger spatial scales. Biological disturbance has been shown to play a role in increasing or maintaining seagrass bed spatial heterogeneity (Valentine et al., 1994; Townsend and Fonseca, 1998). However, it is possible that uniaxial flow may act on the seagrass bed at scales larger than that of individual shoots, as has been discussed thus far. Under uniaxial flow conditions, the seagrass patch edges that face the flow are often the primary eroding portions (Fonseca et al., 1998a,b). Therefore, in addition to shoot expansion normal to the flow, the spread of a seagrass patch spread normal to the flow axis may be exacerbated by a simple probability of reduced disturbance on the patch edges normal to the flow as compared with those facing the flow.

However, self-organized patterns perpendicular to resource gradients have been studied in other communities. Rietkerk et al. (2004) noted that bog patterning perpendicular to ground slope arose from nutrient accumulation mechanisms. As suggested by van de Koppel et al. (2005) for mussel bed banding, a physical scaling factor (in our study, perhaps the enhanced stability arising from shoots arranged in rows) was sufficient to explain a positive, ecological feedback mechanism. What is common among all these studies is that pattern arises not only from the present stimulus, but also on the previous state of the component (hysteresis) – sometimes conflated with "time-averaged conditions". For seagrasses, what is limiting and thus, is being "accumulated" by shoots arrangement (as well as larger scale patterning), is likely simply physical stability, as opposed to nutrients as shown in terrestrial analogs. This effect is congruent with many observations from terrestrial systems where limiting resource accumulation (water, nutrients) is likely the feedback mechanism driving self-organization of vegetation patterns. (See review by Rietkerk et al., 2004). Moreover, Rietkerk et al. (2004) suggest that the presence of community self-organization may be an indicator of community vulnerability; that highly fragmented patterns indicate an inherent vulnerability of the community and that the threat of conversion to an unvegetated state is elevated— and difficult to rebound from. Similar observations have been made for seagrasses in the Beaufort area (Fonseca et al., 2000) where storms differentially impacted seagrass loss dependent on their previous coverage state.

At an intermediate scale of consideration, patch separation may be controlled by length of the downstream wake-defined turbulent structure. Patches may also be driven to self-organize across the landscape in response to the extent and intensity of upstream wakes (*sensu* Folkard, 2005). Such far field interactions, when combined with near field effects that may give rise to individual shoot organization (this study) provides the basis for building a conceptual model of patch arrangement at larger spatial scales (*sensu* Sleeman et al., 2005; Kendrick et al., 2005; e.g., if plants tend to expand across the flow, forming a patch of a certain length-width ratio, then the downstream distance to the next patch would be a consequence of this upstream patch width and the ambient flow regime). However, seagrass beds studied in the Beaufort area experience variable flow directions, both from currents whose direction changes with tidal stage and waves that impinge on the beds from most points of the compass (Fonseca and Bell, 1998). As an apparent consequence, beds near Beaufort tend not to exhibit elongation in any one axis but rather form an anastomosing pattern across the sea floor. The relative rarity of strict uniaxial flow conditions may also be demonstrated by the preponderance of widespread quasi randomly-arranged seagrass shoot patterns that can be observed in nature, an expression of landscape pattern that results not only from shoot arrangement, but other sources of disturbance (e.g., storms, bioturbation) as well (*sensu* den Hartog, 1971: "leopard-skin pattern").

In conclusion, the evidence for flow-induced force reduction and light interception presented here suggests that the organization of seagrass beds at larger spatial scales may be, in no small part, the cumulative result of individual shoots, growing in response to the time-averaged direction (or lack thereof) imposed by hydrodynamic forces. Flow-induced force on individual shoots is increased while sediment stability is enhanced, light interception increased, and ESF maintained as the result of intra-clonal organization with interesting consequences for the expression of various patch shapes and large scale patch spacing across the sea floor.

## Acknowledgments

Jeff Shimeta, Steve Moore and Jason Jedd provided technical guidance in creation and use of critical measuring equipment. Laboratory support at Berkeley was provided by Marlene Martinez, Kim Quillin, and Suzanne Worcester, and in Beaufort by Carolyn Currin, Monica Daniels, Jud Kenworthy, Trish Murphey, Art Schwarzschild, Ed Townsend and Paula Whitfield. The manuscript was improved substantially by reviews of Jud Kenworthy, Carla D'Antonio, Pam Matson, and Wayne Sousa. Final internal reviews by Patti Marraro, Greg Piniak and Amy Uhrin were greatly appreciated. Rigorous comments by two anonymous reviewers for the journal were highly constructive and profoundly changed the theme of the manuscript. Funding was provided by the Department of Integrative Biology at the University of California, Berkeley, and NOAA's National Ocean Service, National Centers for Coastal Ocean Science, Center for Coastal Fisheries and Habitat Research. **[SS]**

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