

In situ measurements of hydrodynamic forces imposed on *Chondrus crispus* Stackhouse

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Abstract

Among the hydrodynamic forces experienced by intertidal organisms, drag and the impingement force are thought to have the greatest effect on macroalgae. These forces are modified by biotic factors such as algal morphology, reconfiguration, and the presence of a canopy. However, much of what is known about the hydrodynamics of macroalgae has been garnered from low-velocity laboratory flume studies. Few field studies have measured drag and none have directly measured the effects of the canopy on force. To examine *in situ* hydrodynamic forces imposed on the turf forming macroalga *Chondrus crispus*, compact digital force sensors were developed that measure and record the 3-dimensional force imposed on a macroalga without disturbing the surrounding canopy. Sensors were positioned within natural *Chondrus* beds and the effects of the canopy, algal morphology, and sea state on *in situ* hydrodynamic force were examined. Additionally, the predictions of a new model for drag on flexible macroalgae were tested by simultaneously measuring force and water velocity. Digital force recordings indicated that *Chondrus* only experience drag; lift and impingement force were negligible in all combinations of factors. Canopies significantly reduced drag by 15–65%. Morphology and size also influenced drag, such that lower forces were imposed on small planar algae than large arborescent individuals. Further, planar algae experienced low drag in all combinations of sea and canopy state, indicating that these individuals may not be as susceptible to wave disturbance as arborescent individuals. Overall, these data indicate that the ability for *Chondrus* to grow large, arborescent individuals is dependent on the drag reducing properties of the canopy, while more hydrodynamically harsh habitats may be accessible to planar morphologies. Additionally, these data suggest that drag models for canopy forming macroalgae must incorporate the effects of the canopy to predict drag accurately *in situ*.

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1. Introduction

Wave-generated hydrodynamic forces are among the most important determinants of rocky-shore intertidal organisms' size and community structure (e.g. Dayton, 1971; Menge, 1976; Paine and Levin, 1981; Denny et al., 1985; Carrington, 2002). Among the forces generated by moving water, lift acts perpendicular to the direction of flow and has been demonstrated to impose force on a variety of sessile invertebrates (e.g. Denny, 1987; Denny

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and Gaylord, 1996). Drag acts parallel to the flow and it has been found to affect invertebrates (e.g. Koehl, 1982; Trussell, 1997) and macroalgae (for review see Denny and Gaylord, 2002). The impingement force, generated by the impact of the face of the wave on an organism, can also be substantial in the intertidal zone (Gaylord, 2000). An additional force, the acceleration reaction, was hypothesized to be important to intertidal organisms (Gaylord et al., 1994), but has since been shown to be negligible due to the small spatial scales at which this force acts on relative to the size of the organisms (Gaylord, 2000). Thus, the effects of drag and the impingement force are thought to be of greatest consequence to intertidal macroalgae (Denny and Gaylord, 2002). These hydrodynamic forces affect the ecology of macroalgae when they exceed an alga's breaking strength and remove the individual (Dudgeon and Johnson, 1992; Carrington et al., 2001; Duggins et al., 2003) or cause damage to an individual (Blanchette, 1997).

The drag experienced by an intertidal organism depends on the velocity of the water relative to the organism and biological factors such as the size and shape of the organism (Vogel, 1994). Drag increases with velocity squared (U^2), and is directly proportional to the size of the organism, usually measured as the frontal area (the area projected into the flow) for rigid organisms or planform area (see Johnson, 2001) for flexible organisms like macroalgae. Additionally, drag is proportional to the drag coefficient (C_D), which accounts for the interaction between the shape of the organism and the flow moving past it.

Several aspects of the biology of macroalgae can influence drag. For example, the flexibility of macroalgae can influence the velocity of water relative to their thalli. Large macroalgae can bend and move with the flow such that the relative velocity is low, and drag is reduced (Koehl, 1984, 1986, 1999; Koehl and Alberte, 1988; Gaylord and Denny, 1997; Denny et al., 1997; Stewart, 2004). Flexibility can also influence the size and shape of a macroalga by a process called reconfiguration, where an alga can assume a smaller and/or more streamlined posture at high flows than expected from their low-velocity size or planform area (Vogel, 1994; Carrington, 1990; Johnson, 2001; Gaylord, 2000; Boller and Carrington, 2006). Additionally, morphological (shape) variation within and among species affects the drag coefficient such that some species generate more drag than others (e.g. Gerard and Mann, 1979; Koehl and Alberte, 1988; Dudgeon and Johnson, 1992; Blanchette, 1997; Denny et al., 1997; Pratt and Johnson, 2002; Stewart and Carpenter, 2003; but see Carrington, 1990).

The aggregation of macroalgae in canopies can also affect their hydrodynamics. Macroalgae within a canopy experience reduced water velocities when they draft in the wake of neighbors (Eckman et al., 1989; Johnson, 2001; but see Holbrook et al., 1991). However, the few studies that have specifically examined the effects of the canopy on hydrodynamic force have been conducted in the laboratory. Johnson (2001) demonstrated that the presence of a single individual upstream can reduce drag on *Chondrus crispus* by 65% and individuals in the center of a canopy of several individuals experienced 83% lower force at velocities up to 0.45 m s^{-1} (typical of subtidal canopies). Additionally, the mechanical support by neighbors can reduce the force experienced by an individual (Johnson, 2001). Further, Stevens et al. (2004) used computational models to predict a 30% reduction in maximum force on individuals in beds of the intertidal kelp *Durvillaea antarctica* via the interaction of blades with neighbors. Conversely, Carrington (1990) saw only a small, non-significant reduction in drag at $3\text{--}4 \text{ m s}^{-1}$ for an entire group of *Mastocarpus papillatus* compared to those same individuals measured separately. Thus it is unclear if the canopy will have an effect for small macroalgae in the high water velocities of the rocky intertidal zone. Direct measurements of the hydrodynamic forces and the effect of the canopy on those forces are needed.

Examining the effects of the canopy in the field poses several technological challenges. To date, few field studies have measured hydrodynamic force imposed on macroalgae and none have measured the effects of canopies *in situ*. Gaylord and Denny (1997) measured the bending moments imposed on individual *Pterygophora californica* in the field using a custom-made torsion cylinder and datalogger. Gaylord (1999) measured force experienced by the intertidal rockweed *Pelvetia compressa* with a 2-axis cantilever-style force transducer wired to a computer. Stevens et al. (2002) measured *in situ* force, acceleration and displacement on wave exposed *D. antarctica* using sensors cabled to a data logging system in the supratidal zone. Stewart (2004) measured the effects of buoyancy and flexural stiffness on the subtidal alga, *Tubinaria ornata*, using a force transducer system tethered to a boat.

While these studies provided detailed digital measurements of the forces imposed on macroalgae, the devices used to collect the data could not be used to address the influence of small, wave-swept, intertidal canopies due to their large size and the invasive nature of their deployment. However, the design and deployment of very small autonomous devices that sense and record the force imposed on an intertidal organism is now

possible due to the availability of low cost miniature surface-mount components, high-quality and inexpensive printed circuit boards, and advanced but accessible software development tools. In this study, miniature autonomous hydrodynamic force sensors were developed to measure the forces imposed on *Chondrus crispus* Stackhouse in natural, intact canopies and cleared areas. Specifically, the effects of the canopy, algal morphology, and sea state on hydrodynamic force were evaluated. Additionally, the predictions of the reconfiguration drag model (Boller and Carrington, 2006) were tested in the field.

2. Materials and methods

2.1. Hydrodynamic force sensor

Hydrodynamic forces were measured using 3-axis digital force sensors specially designed to be deployed within the canopy (Fig. 1; Boller, 2005). The constraints of the experiment dictated that the sensor be as compact as possible and autonomous (i.e. contain the sensor, data storage and power supply). Each sensor (Fig. 2) consisted of a 3 axis ceramic force transducer (Series109 3D TrackStick, CTS Corp., Elkhart, IN; normally used as a mouse pointing device), three AD623 instrumentation amplifiers (Analog Devices Inc., Norwood, MA), a PIC16LF818 microcontroller unit (Microchip Corp., Chandler, AZ), a real-time clock circuit, and four 24AA512 EEPROM memory chips (Microchip Corp., Chandler, AZ). The components were assembled on a custom four-layer circuit board and packaged in a waterproof housing. The sensor program was written in assembly language using MPLAB software (ver. 6.20, Microchip Corp., Chandler, AZ), and an ICD2 in-circuit debugger (Microchip Corp., Chandler, AZ) was used to program the sensors.

The basic design of the circuit was as follows (Fig. 2). The force signal from each axis of the force transducer was amplified with a separate instrumentation amplifier. The amplified forces were then converted from analog to digital signals using the microcontroller unit's on-chip 10 bit analog-to-digital (A/D) converter. The three 10 bit digital values were packaged into four bytes and sent serially from the microcontroller unit to the EEPROMs for storage using the I²C communication protocol (Irazabal and Blozis, 2003). The three separate values were later reconstructed during the processing of the raw data. The microcontroller unit program allowed for the use of a real-time clock delay timer to synchronize the start of data collection for several sensors. Data were recorded

from each axis at 120 Hz in order to sense the maximum force generated by a wave as it broke and washed over the sensor. This recording rate limited the length of experimental runs to ~9 min (~64,000 data points) due to the memory space available.

A 3 mm plastic post was attached to the ceramic force transducer to provide a platform for the attachment of individual algae (Fig. 1). The post extended the moment arm of the sensor, thereby increasing sensitivity for the *x* and *y* axes. Each sensor was calibrated separately by hanging weights from strings affixed to the top surface of the platform. Due to small differences in the total length of the moment arms, specific calibrations curves were used for each sensor, ranging from 0.153 to 0.172 N per A/D bit.

Additionally, sensors were modified to measure the water velocities at the experimental sites. A 1.27 cm diameter roughened plastic sphere was attached to a 4 mm post and affixed to the ceramic force transducer. The velocity sensor was calibrated by hanging weights from the center of the sphere and by measuring the force exerted on the sphere in a flow tank at velocities ranging from 0 to 3 m s⁻¹. The greater extension of the moment arm of the force transducer makes the water velocity sensor more sensitive but also more fragile (breakage of the ceramic post). Thus water velocity data were not collected for all experimental runs due to the failure of the sensors.

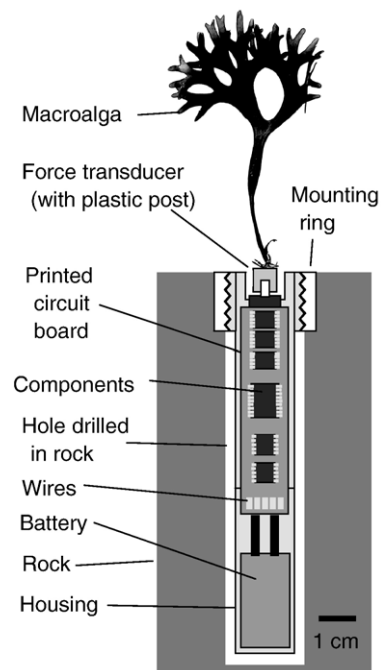


Fig. 1. Details of the hydrodynamic force sensor.

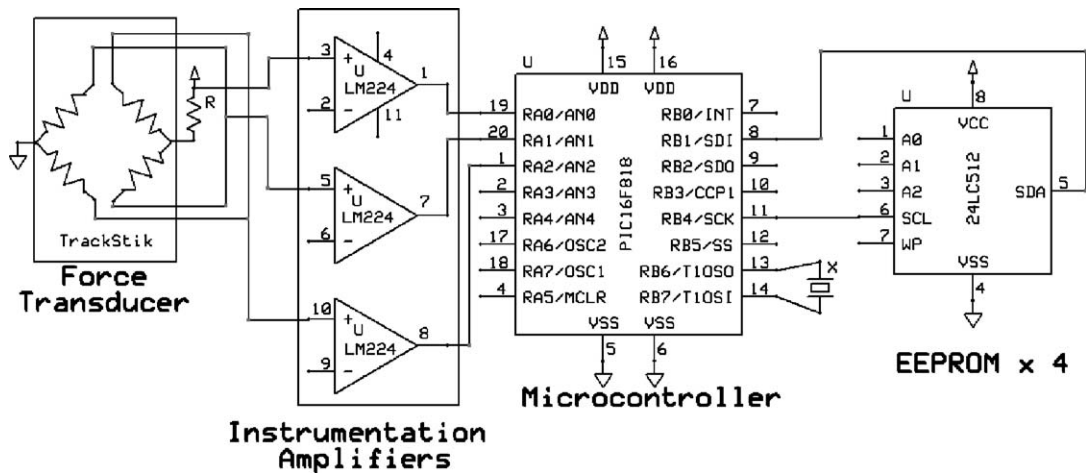


Fig. 2. Simplified schematic of the force sensor circuit. Signals from the force transducer were amplified via the three instrumentation amplifiers to the microcontroller unit (MCU). The MCU controlled the start time, stop time, and frequency of measurements, and then passed the data to the four EEPROM for storage.

Waterproof housings for the sensors were built from 1.27 cm (1/2 in.) CPVC water supply pipe, 1.27 cm male threaded PVC fittings, and solid CPVC rod stock (Fig. 1). Each consisted of two 6 cm sections of pipe that housed the electronic components and battery, respectively. The lower battery section was reamed to an inside diameter of 14.4 mm to accommodate the 13.9 mm diameter battery. One end of this section was plugged with solid CPVC rod stock that was glued in place with CPVC cement. The upper electronic component section of the housing had a 14.4 mm outside diameter flange at the bottom that fit snugly inside the battery section. A male threaded PVC fitting was reamed and glued around the top end of the component section. All but the threads of the fitting were then cut off such that the sensor sat flush with the mount when deployed. The force transducer end of the circuit board was countersunk flush with the end of the housing and sealed in position using five-minute plastic welding epoxy (Devcon Corp., Riviera Beach, FL). For a waterproof deployment, the two halves were fit together with silicon grease and wrapped with a 2 cm wide strip of Parafilm (American National Can, Neenah, WI) to seal the seam.

Sensors interfaced with a PC using an Aardvark I²C/SPI USB interface (TotalPhase Inc., Sunnyvale, CA). To launch each sensor, the real-time clock parameters were programmed into the first EEPROM. Upon the startup of the microcontroller, setup parameters were read into memory and used to set the current and data logging start times. After deployment, data were retrieved and saved from the memory chips via the Aardvark interface.

Raw data files were reconstructed into *x*-, *y*- and *z*-axis data in MatLab (Mathworks Inc., Natick, MA). These raw data (in bits) were converted to force using the calibration curves prepared for each sensor and the direction of the force vector was determined from the relative magnitudes of each axis. The peak forces in 10 s intervals were determined and used in subsequent statistical analyses.

2.2. Sensor deployment

Experiments were conducted in *Chondrus* beds adjacent to Bass Rock in Rhode Island Sound (41.40°N, 71.45°W). Hydrodynamic force sensors were positioned in established intertidal canopies, minimizing the disturbance to the surrounding algae. Each sensor was mounted in a 1.6 cm diameter, 11 cm deep hole drilled in the rock using a battery-powered masonry hammer drill (TE 6-A, Hilti, Inc., Tulsa, OK). Threaded PVC mounting rings were countersunk directly above the holes and affixed to the rock with Z-Spar Splash Zone Epoxy (Kop-Coat Inc., Pittsburgh, PA) such that the platforms were approximately flush with the substrate (Fig. 1) and only a 4 cm diameter gap was created within the canopy. Canopy treatments were left untouched with all surrounding algae in place. Canopy removal treatments (hereafter called “Solitary”) were created by scraping away the surrounding 15 cm of canopy with a wide masonry chisel, making a 30 cm diameter gap.

Each sensor was deployed in the intertidal during similar tide heights for approximately 10 to 15 min in order to complete the 9 min data collection but minimize

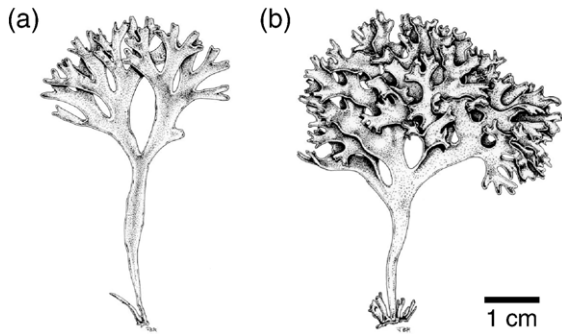


Fig. 3. Representative morphotypes of *Chondrus* used in the experiments. (a) Planar morphotype, with few branches all of which lie in one plane. (b) Arborescent morphotypes, with many branches growing in three-dimensions.

algal/glue and sensor failure. Algae were collected and affixed to the sensors in the field. Sensors were launched with a notebook PC, sealed, and then placed in ambient seawater for 2 to 5 min to allow the temperature within the housing and the force transducer to equilibrate (to prevent temperature drift). Sensors were then seated in the mounting holes by wading in the submerged intertidal among the breaking waves and carefully screwing the sensors in place. Data collection was started automatically by the timer and sensors were retrieved from the intertidal after the recording session was completed. The housings were then dried and opened, and sensors were connected to the PC for data retrieval. This procedure was repeated for a maximum of six cycles during 15 low tides in which the waves were breaking on the site. This procedure precluded the ability to measure forces on high surf days due to safety concerns.

2.3. Oceanographic data

Significant wave height (H_S) was measured offshore of Bass Rock over the course of the experiments using a SBE26 Seagauge (Sea Bird Electronics, Bellevue, WA). H_S is the average of the highest 1/3 waves over a time period and is used to describe the distribution of wave heights (Denny, 1988). The Seagauge was mounted approximately 200 m offshore from the study site at 7 m depth and recorded 20 min of 2 Hz pressure data every 4 h for a total of 6 bursts per day. H_S for each burst was calculated using Seasoft software (Seabird Electronics, Bellevue, WA) and daily averages were calculated. Additionally, visual observations of size and location of waves breaking on the experimental sites were recorded. These data were used to classify the sea states among experimental days.

2.4. Algal collection

Individual *Chondrus* were collected by removing the alga and a small portion of the underlying rock with a hammer and chisel. The holdfast of each individual was carefully dissected from the rock so as to not damage the holdfast and stipe/holdfast junction and trimmed with a razor blade to a flat surface. Algae were then affixed to the force platform of the sensor with cyanoacrylate glue such that their bending was not affected by the glue.

Chondrus morphology is variable and two extreme morphotypes (planar and arborescent; Fig. 3) were used for the experiments to maximize the hypothesized effects of morphology. Planar individuals had smaller areas, fewer branches and were roughly two-dimensional. Arborescent colonies had larger areas and were highly branched in three dimensions. It is important to note that, in this study, the size of the alga was not separated from the morphology (as in Carrington, 1990) because arborescent individuals were always larger, and large-area planar algae do not occur. All individuals used in the study were examined in the same canopy from which they were collected and samples and canopies were chosen to have similar heights (6 to 8 cm). Each alga was digitally photographed before each experimental run and then examined after the experiment to confirm that no loss of tissue occurred during the run. The size of each individual was measured from the digital photo as the area of the alga as it lay flat on its side. Area measurements were made with ImageJ software (ver. 1.33, National Institutes of Health, Bethesda,

Table 1
Summary of sea state conditions for each experiment

Experiment	Treatment	Date	H_S (m)		
			Mean	Min	Max
Canopy removal	(1, 2, and 3)	11/07/2004	0.59	0.43	0.79
Canopy removal	(4 and 5)	11/24/2004	1.01	0.68	1.57
Morphology and sea state	Calm	10/13/2004	0.27	0.23	0.33
Morphology and sea state	Wavy	10/16/2004	1.24	0.83	1.64
Morphology and sea state	Wavy	10/17/2004	1.05	0.89	1.28
Morphology and sea state	Wavy	10/27/2004	0.76	0.69	0.80
Morphology and sea state	Calm	10/29/2004	0.72	0.61	0.82
		October	0.78	0.23	2.18
		November	0.67	0.13	2.67

$N=6$ for each day. For comparison, monthly statistics are presented at the bottom of the table.

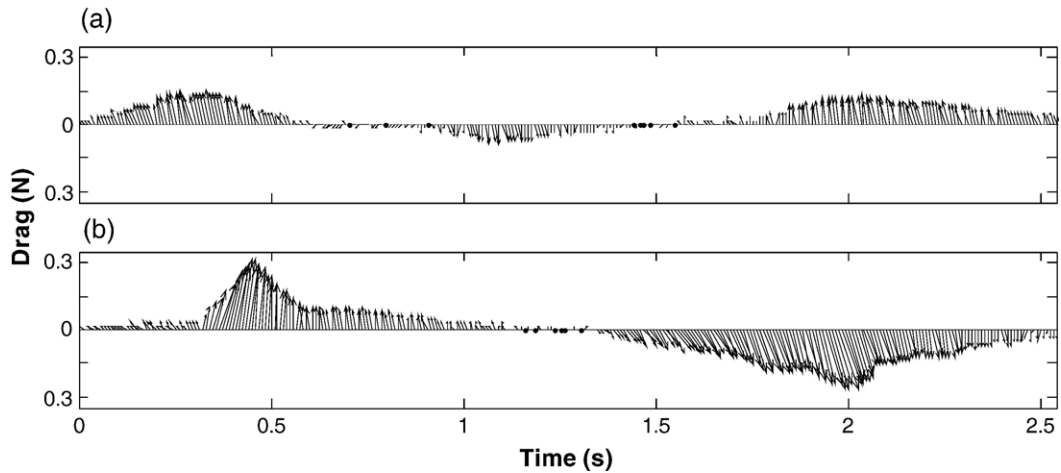


Fig. 4. Representative time series of wave forces on *Chondrus* in the field on 7 November 2004. Each arrow represents the magnitude and direction of a force. (a) Arborescent alga in a canopy. (b) Arborescent alga in solitary position. Note that the directions are relative to the arbitrary orientation of the sensor and do not necessarily correspond to a specific compass bearing.

MD). Life-history phase was identified in the laboratory after the field experiments using a resorcinol test (Garbary and DeWreede, 1988).

2.5. Experimental designs

The hydrodynamic force and its dependence on algal canopy, algal morphology and sea state were examined in two separate experiments. Each experiment consisted of several data collection sessions (Table 1). The canopy experiment examined the effects of the canopy on drag in arborescent *Chondrus*. Forces were measured on five algae with the surrounding canopy intact. Sensors were then retrieved and downloaded and the surrounding canopy was scraped from around the sensor mount with

a chisel. Sensors were redeployed to the same site and forces were again measured on the same alga. By examining an alga in the same location and sea state (same tidal cycle) under both canopy and solitary conditions, the effects of the temporal variation in water velocities (due to differences in waviness among days) were minimized between treatments. A paired t-test was used to examine the effect of the removal of the canopy (Systat 11.0, Systat Software Inc., Point Richmond, CA).

The effects of morphology and sea state on drag were examined in separate canopy and solitary sites. Force was measured on a total of seven arborescent and eight planar algae in both wavy and calm sea states at each site. In this experiment, the solitary site was established

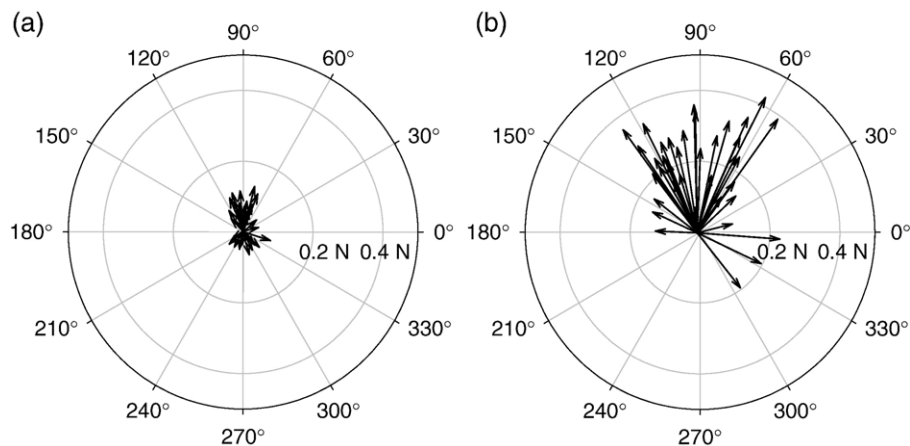


Fig. 5. Magnitudes and relative directions of peak forces experienced by a representative arborescent alga in the canopy experiment on 7 November 2004. The length of each arrow represents the peak force (N) recorded in a 10 s interval: (a) canopy; (b) solitary. Note that the directions are relative to the arbitrary orientation of the sensor and do not necessarily correspond to any compass bearing.

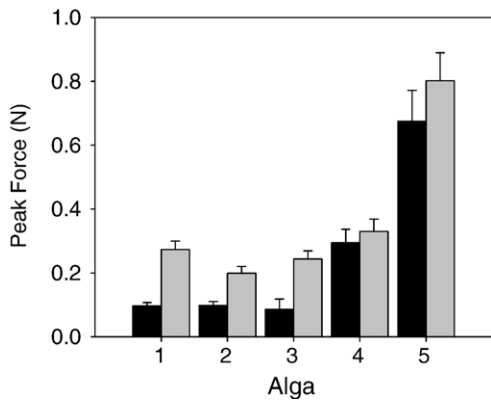


Fig. 6. Drag on individual macroalgae in canopy (black) and solitary (gray) positions. Bars are mean of peak force during 10 s intervals ($\pm 95\%$ CI, $N=28$ to 52). Removal of the canopy significantly increased the forces experienced by individuals (paired t -test: $t = -4.854$, $df=4$, $p < 0.01$).

by clearing the surrounding algae prior to the start of the experiment, while the canopy site was left intact. This design controlled for microhabitat variation. However, due to variation in water flow between the sites, canopy and solitary data were analyzed separately as two-factor ANOVAs and Tukey’s post hoc comparisons were performed in Systat. Thus, the effect of the canopy, and the interactions related to it, were not examined in this second experiment.

Additionally, water velocity data were collected simultaneously with algal force for a subset of arborescent algae. These data were collected to examine the relationship between the force measured in the field and that predicted by the reconfiguration drag model (Boller and Carrington, 2006). Water velocity was recorded from a sensor mounted directly between the canopy and solitary sites of the morphology and sea state experiment with a modified force sensor. Because the waves hit each sensor at slightly different times, the peak velocity was determined for each 10 s interval (see above) and matched with the concurrent peak algal force for that interval. A predicted force curve for each alga was calculated using the reconfiguration drag model (Boller

Table 2
Results from the ANOVA of sea state and morphology experiment for solitary individuals

Source	Sum-of-squares	df	Mean-square	F-ratio	P
Sea state	0.064	1	0.064	2.906	0.116
Morphology	0.264	1	0.264	11.951	0.005
Morphology \times Sea state	0.029	1	0.029	1.293	0.280
Error	0.243	11	0.022		

The bold value indicates a significant morphology effect.

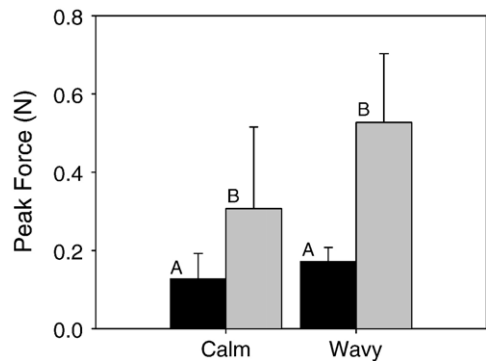


Fig. 7. Drag on planar (black) and arborescent (gray) macroalgae in the solitary position under calm and wavy conditions. Columns represent mean of peak force of 10 s intervals ($\pm 95\%$ CI, $N=3$ to 4). Letters above columns denote the groups defined by post hoc tests. Drag on arborescent algae is significantly higher than planar algae, regardless of sea state. The effect of sea state alone was not significant.

and Carrington, 2006). With the model, drag (F_{DR}) was predicted using the equation:

$$F_{DR} = 1/2\rho U^2 A_{rep} a_U C_U \tag{1}$$

where ρ was the density of sea water (1025 kg m^{-3}), U was the velocity of the water relative to the alga (m s^{-1}), A_{rep} was the representative area of the alga at low reconfiguration (m^2), a_U was normalized area as a function of velocity, C_U was the drag coefficient as a function of velocity. Area parameters used were 0.44, 0.75, and 0.70 m s^{-1} for a_{∞} , a_R , and β_a , respectively. C_D parameters were 0.75, 0.87, and 0.42 m s^{-1} for C_{∞} , C_R , and β_C , respectively (see Boller and Carrington, 2006 for further explanation of variables). A_{rep} was estimated as the area of the algae measured from the photo taken in the field.

3. Results

Sea state at Bass Rock varied considerably within and among days. Significant wave height (H_S) measured

Table 3
Results from the ANOVA of sea state and morphology experiment in the canopy

Source	Sum-of-squares	df	Mean-square	F-ratio	P
Sea state	0.019	1	0.019	12.352	0.005
Morphology	0.030	1	0.030	19.676	0.001
Morphology \times Sea state	0.036	1	0.036	23.476	0.001
Error	0.017	11	0.002		

The bold value indicates a significant morphology by sea state interaction.

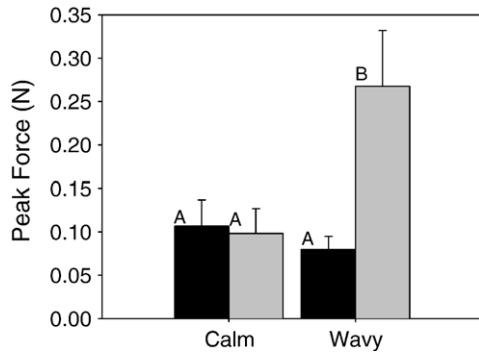


Fig. 8. Drag on planar (black) and arborescent (gray) macroalgae in the canopy under calm and wavy conditions. Columns represent mean of peak force of 10 s intervals ($\pm 95\%$ CI, $N=3$ to 4). Letters above columns denote the groups defined by post hoc tests. Forces were significantly higher on arborescent algae in wavy conditions than in all other combinations of factors.

offshore ranged from 0.13 to 2.67 m in the 2 months in which the study was conducted (Table 1). Average H_S ranged from 0.27 to 0.72 m on “calm” days and from 0.76 to 1.24 m on “wavy” days used in these experiments. Visual observations indicated that waves on calm days were small, breaking right on or near the sites. In contrast, wavy days had large waves that broke several meters offshore of the sites that turned into bores that washed over the sites. While the difference in H_S on October 27th and 29th is small (0.04 m), visual observations support the designation of these two dates as wavy and calm, respectively. This discrepancy is likely due to the local topography and variation in swell direction, such that the site was more protected from the direction of wave action on October 29th.

Overall, drag on individual algae tended to have a dominant plane of force within individual wave events

(Fig. 4). Forces measured in the vertical direction were minimal for all of the algae, indicating that these organisms do not experience substantial lift. When in the canopy, peak forces were small and variable in direction (Fig. 5a). In contrast, peak forces for algae in a solitary position were larger and tended to cluster in one general direction, presumably aligning with the dominant direction of the waves (Fig. 5b). Some peak forces occurred in the opposite direction, indicating the returning wash of water offshore can also generate high forces. When tested explicitly, canopies significantly reduced the average peak drag experienced by arborescent *Chondrus* 15% to 65% (paired t -test: $t=-4.854$, $df=4$, $p<0.01$; Fig. 6).

For solitary algae in the morphology/sea state experiment, drag varied significantly with morphology but not with sea state (Table 2). When solitary, drag on arborescent algae was 2 to 3 times higher than on planar algae (Fig. 7). The magnitude of this difference may be an underestimate because the combination of the wavy sea state, arborescent algae and solitary position resulted in several individuals breaking at the stipe before force measurements were recorded. No other algae were lost due to stipe failure in any other combinations of factors. For algae in the canopy, drag was significantly influenced by the interaction of the morphology with sea state (Table 3). Pairwise comparisons indicated that forces on arborescent algae in the wavy sea state were 2.8 times higher than in all other combinations of factors in the canopy (Fig. 8).

When recorded concurrently, peak water velocity and algal force ranged from 0.33 to 4.10 m s^{-1} and 0.04 to 2.49 N, respectively (Fig. 9). Predictions of the reconfiguration drag model (Eq. (1)) were similar to the highest forces recorded at any particular velocity for

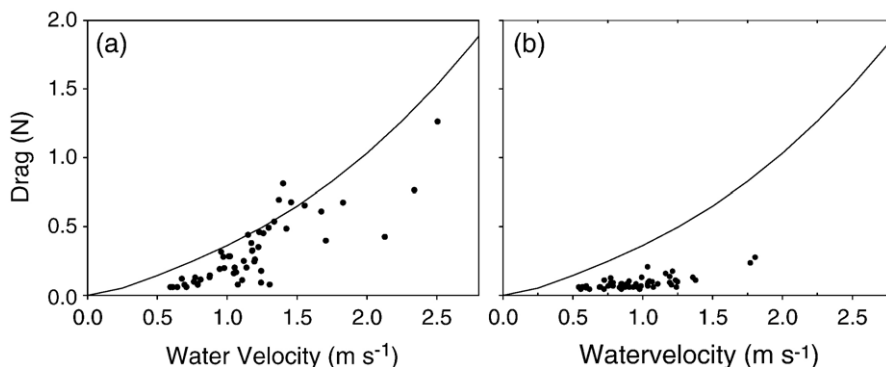


Fig. 9. Drag with respect to water velocity for a representative *Chondrus* in (a) solitary and (b) canopy positions measured on 13 October 2004. Each data point represents the peak force and water velocity measured during a 10 s interval. Predictions (lines) were generated based on the size of the macroalga using the reconfiguration drag model.

solitary individuals (Fig. 9a). Overall, 41% of the forces fell within $\pm 50\%$ of the predicted value for solitary algae. In contrast, model predictions consistently overestimated drag for canopy algae (Fig. 9b). Only 7% of observations were within $\pm 50\%$, with some observations as low as 5% of the predicted value.

4. Discussion

The ability to measure hydrodynamic forces imposed on a macroalga in its natural habitat is essential to resolving how these rocky intertidal organisms are influenced by their physical surroundings. The sensors designed for this study allowed for the precise measurement of hydrodynamic force with little alteration of the surrounding habitat. These data provide new insights on the types of hydrodynamic forces imposed on intertidal *Chondrus* and how biological factors influence those forces. In addition, the sensor allowed for the first field test of a new model of drag generation for flexible organisms.

4.1. *In situ* digital hydrodynamic force measurements

In detailed three-dimensional measurements of hydrodynamic forces imposed on *Chondrus*, drag was the only significant force observed. Forces measured in this study tended to build consistently to a peak (Fig. 4) and lacked a large initial peak force observed during the first 0.5 s of the waves (the hallmark of a strong impingement force; Gaylord, 2000) despite the fact that the algae were often exposed to the air immediately prior to the breaking of the waves on the alga. The lack of impingement force may be due to the reconfiguration of the alga (or the entire canopy) as the wave first hits. If the duration of the impingement force is shorter than the time it takes to reconfigure the alga, the impingement force will not be transmitted to the stipe or sensor (as per Koehl, 1982, 1984, 1986). The similarity between the maximum forces measured and predicted drag for solitary algae (Fig. 9a) also suggests that impingement forces are not a factor for *Chondrus*; maximum forces rarely exceed the force predicted by a drag model that lacks an impingement force term.

Johnson (2001) detected a velocity difference within and above the canopy, suggesting that a pressure differential could cause lift in a manner similar to the flow skimming over mussel beds (Denny, 1987). However, no vertical forces were measured in this study, either in or out of the canopy, indicating the absence of lift. Thus any pressure differential developed by the canopy was too small to produce a detectable force.

Algae generally experienced bidirectional forces in each wave event (Fig. 4). Due to the difficulty in placing the sensors in their mounts while the waves were breaking, the precise orientation of forces relative to the shore is not known. However, observations of the waves suggest that forces are predominantly perpendicular to the shore. The dominant onshore flow was often followed by the offshore down-surge of the wave. Despite the turbulent nature of the flow of a breaking or broken wave, vectors indicate that direction of force was consistent or changed in a steady manner as the wave passed (Fig. 4). This is consistent with previous findings (Gaylord, 2000), in which velocities were found to have spatial scales of 0.2 to 0.5 m.

4.2. Canopy effects

This study is the first *in situ* examination of the influence of the canopy on the drag experienced by an intertidal macroalga. Canopies have a strong effect on drag, reducing forces by 15% to 65% compared to solitary individuals (Fig. 6). This ameliorating effect was previously only demonstrated in low velocity flows (Johnson, 2001). It is possible that the effects of the canopy reported here may be an underestimate because the area removed from around the solitary individual was limited. However, a study of the edge effects of mussel beds (O'Donnell, 2006) demonstrated that little difference in hydrodynamic force was seen between a 30 cm gap and gaps much larger than 30 cm, suggesting any edge effect of the surrounding canopy is limited.

The ameliorating effect of the canopy may promote the growth of arborescent individuals in the intertidal. *Chondrus* dislodge when their stipes fail and, due to the underscaling of stipe strength with macroalgal size in *Chondrus* and other species (Carrington, 1990; Dudgeon and Johnson, 1992), the probability of dislodgement increases with size. Thus arborescent individuals are more likely to dislodge and should not be present in wavy areas. However, the reduction of drag by the canopy reduces the forces transmitted to the stipe, and allows arborescent individuals to persist in wavier habitats. Thus habitat amelioration by the canopy is likely responsible for the presence of arborescent individuals in populations where models predict their dislodgement (Pratt and Johnson, 2002).

Not only does the canopy provide protection during storms, but it likely protects arborescent individuals under moderate conditions as well. This study was conducted during only moderately wavy sea states. Yet, the forces on arborescent fronds in solitary position approached the lower range of the breaking strength of

the stipe (~ 2 N, Carrington et al., 2001) and some solitary algae were broken by waves before forces could be measured. However, protection from dislodgment by the canopy is not absolute, as is evident by occasional high force measured in the canopy in this study (Fig. 9b) and the extensive winter dislodgment of individuals (Dudgeon and Johnson, 1992). Overall, the forces recorded on solitary individuals in this study exceeded strength of *Chondrus* stipes reported in previous studies (Carrington et al., 2001), suggesting that without the canopy, arborescent *Chondrus* would not persist in the intertidal zone.

4.3. Morphology and sea state effects

Drag on small planar individuals was small (~ 0.1 N) regardless of sea state (Figs. 7 and 8). In fact, planar individuals experienced forces that are at least an order of magnitude lower than the breaking strength of an individual, with or without the canopy in wavy conditions. This suggested that small planar morphologies can exploit wave-exposed areas. Indeed, very exposed areas in Rhode Island often have fairly sparse canopies of relatively planar individuals (M. Boller, personal observations), suggesting that large arborescent individuals are unable to survive. Additionally, on newly-formed habitats (e.g., overturned boulders and scoured areas) or crusts that have had all the fronds removed, planar individuals could grow and develop into the canopy needed for the establishment of larger, arborescent morphologies. Investigations of the “ontogeny” of morphologies in a newly formed canopy could identify such a succession process.

Despite the apparent direct relationship between wave height, water velocity and drag (but see Helmuth and Denny, 2003), the influence of sea state was not always evident in this study. Higher sea states cause larger forces for arborescent individuals in the canopy (Fig. 8) but this effect is not present for solitary algae (Fig. 7). Forces on solitary arborescent algae in high and low sea states are statistically indistinguishable. The lack of a relationship between sea state and drag may be due to the relatively moderate conditions of the experiment; water velocities in stormy conditions would be much higher (>10 m s⁻¹, Denny et al., 2003). Additionally, the effectiveness of the canopy in reducing force on arborescent algae may decrease with even a moderate increase in sea state. In the canopy experiment, a smaller reduction in force was observed during higher sea state ($H_S=1.01$ m; algae 4 and 5 in Fig. 6) than in the lower sea state ($H_S=0.59$ m; algae 1, 2, and 3 in Fig. 6). However, a larger sample size is

needed to properly test for the interaction between sea state and canopy.

4.4. Test of reconfiguration drag model

Forces measured on solitary algae at a particular water velocity were variable, but 41% of field observations were within $\pm 50\%$ of forces predicted by the reconfiguration drag model (Fig. 6). The highest forces at any velocity rarely exceed predicted forces. The underestimation of force may be due to one or more sources of error. First, a relatively small patch of canopy was removed to create the solitary site; some force reducing effect of the canopy may have been present for some waves. Second, the duration of wave events may have been short enough that algae were still in the process of realigning with the flow when the maximum velocity was reached, resulting in a lower force being transmitted to the holdfast. Third, water velocity was measured a few cm above the position of the reconfigured alga; a benthic boundary layer may have caused lower velocities at the level of the alga, resulting in lower force than predicted. Further, these results were similar to Gaylord (2000), where the drag generated by newly breaking waves was lower than predicted by hydrodynamic models, while drag from developed bores and down-surge from waves matched predictions more closely.

In contrast to solitary *Chondrus*, drag on individuals in the canopy was poorly predicted by the reconfiguration model (Fig. 9b). Increasing flow velocity measured outside the canopy had little effect on drag; at high water velocities, measured drag was an order of magnitude lower than predicted by the model (Fig. 9b). Thus, canopies reduce the force exerted on individuals, and the effect of canopies should be incorporated into any model used to predict force on canopy forming macroalgae.

5. Conclusions

The examination of hydrodynamic force *in situ* is essential for the understanding of how organisms interact with the harsh environment of the wave-swept rocky intertidal. The miniature, autonomous electronic sensors developed in this study were the first to measure the influence of the canopy *in situ*. Drag, the primary hydrodynamic force imposed on *Chondrus*, was significantly reduced by the presence of a canopy. The canopy enables arborescent individuals to thrive in an environment that would otherwise be too physically harsh. Drag on planar algae, however, was lower overall and makes them less sensitive to the hydrodynamic environment, which may allow this morphology to exploit a broader

range of intertidal habitats. Last, the reconfiguration drag model predicted drag on solitary *Chondrus* well, but results suggest that drag models for canopy forming macroalgae must consider the ameliorating effects of the canopy to predict accurately drag *in situ*.

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