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Size, not morphology, determines hydrodynamic performance of a kelp during peak flow

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Abstract The morphology and shape of algae can affect their survival in wave-swept environments because of the hydrodynamic drag created by water flow. Studies of morphology and drag are typically conducted at relatively low water velocities, and the influence of algal morphology on drag, over the range of water velocities algae must cope with in their natural environment, remains unclear. Here, we tested the link between morphological variation and hydrodynamic drag for a dominant kelp with complex morphology (*Ecklonia radiata*), over a range of water velocities representative of conditions on wave-swept reefs. Our results indicated that kelps on subtidal reefs must withstand maximal orbital water velocities in excess of 2–3 m s^{-1}. Our measurements of drag, resulting from flows ranging from 1 to 3 m s^{-1}, revealed that shape- and width-related thallus and lamina characters were important to drag at low speed, but that total thallus area (or biomass) was the main determinant of drag at high flow. Drag coefficients converged at increasing speed suggesting that, at high flow, significant thallus reconfiguration (more streamlined shape) decoupled drag from morphology. This implies that, at peak velocities, only size (total area), not morphology, is important to drag and the probability of dislodgment.

Introduction

Important questions in ecology and evolution centre on the relationship between an organism's morphology and its performance. Different morphological characters can lead to different performances, making a specific morphology more suitable to a given environment through enhanced survival and fitness (Koehl 1996; Wainwright 1996). For sessile marine organisms, morphology has critical implications for their likelihood of dislodgment or survival when experiencing intense hydrodynamic forces, driven by waves and currents (Denny 2006). Macroalgae such as kelps are found across different hydrodynamic environments and exhibit great intra- and inter-specific morphological variation (Johnson and Koehl 1994; Roberson and Coyer 2004; Wernberg and Vanderklift 2010). Consequently, they are good models for studying the ecological implications of morphology.

Differences in algal morphology are thought to be the consequence of a trade-off between limiting drag forces, which prevent breakage and dislodgement for wave exposed morphotypes (Kawamata 2001; Blanchette et al. 2002; Buck and Buchholz 2005) and maximizing light capture and transfer of gas and nutrients for photosynthesis and growth for sheltered morphotypes (Koehl and Alberte 1988; Stewart and Carpenter 2003; Haring and Carpenter 2007). Therefore, it is generally accepted that algae from

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sheltered environments have wide, thin and undulate thalli which are often bushy, whereas algae from exposed environments have narrow, thick and flat thalli with thick stipes and a more streamlined shape. Several studies have demonstrated that the hydrodynamic forces resulting from waves are strong drivers of this variation (Wernberg and Thomsen 2005; Fowler-Walker et al. 2006; Wernberg and Vanderklift 2010; Krumhansl and Scheibling 2011), either as a consequence of pruning and tattering (Dudgeon and Johnson 1992; Blanchette 1997; Carrington et al. 2001; Mach et al. 2007), which limit size and shape mechanically, or as a consequence of genotypic or phenotypic adaptation towards characters that minimize hydrodynamic drag (Fowler-Walker et al. 2006; Krumhansl and Scheibling 2011). The major physical force acting on a subtidal kelp is the hydrodynamic drag, created by water flow, which pulls the alga downstream (Gaylord et al. 1994; Denny and Gaylord 2002). The magnitude of the force is proportional to the velocity of the water and depends on the size and shape of the alga (Vogel 1984; Denny 1995; Thomsen et al. 2004). Moreover, the shape of most algae can reconfigure in response to increasing flow into a more streamlined and homogeneous shape ('reconfiguration', Vogel 1994; Harder et al. 2004; Wernberg 2005), and the effects of morphology on drag may therefore change with water velocity.

The kelp *Ecklonia radiata* (C. Agardh) J. Agardh is a dominant habitat-former on the temperate subtidal reefs of Australasia (Wernberg et al. 2003b; Fowler-Walker et al. 2006; Connell and Irving 2008). *E. radiata* is probably the most abundant macroalga in Australia, and it forms large beds on moderate- to rough-water coasts (Connell and Irving 2008; Wernberg and Connell 2008). It can reach a length up to 2 m and has a thallus with a terete basal stipe that bears a flattened blade with ramified lateral branches which often create a complex 3-dimensional shape (Wernberg et al. 2003a). Despite extensive knowledge of the relationships between wave exposure and morphological variation for this species (Wernberg and Thomsen 2005; Fowler-Walker et al. 2006; Wernberg and Vanderklift 2010), little is known about how this affects drag. In this study, we tested how morphological variations and shape affect the hydrodynamic drag experienced under different hydrodynamic conditions and more specifically at velocities typical of storms.

To test our main hypothesis, that morphological changes affect the hydrodynamic drag, and to determine whether there is 'an object area' to be incorporated in the drag equation (Eq. 2) for *E. radiata,* we subjected thalli of differing morphologies to a range of water velocities, representative of field conditions, and measured the resultant drag. Ultimately, we tested whether the coefficient of drag changes with water velocity.

Materials and methods

Water velocities

The measurements took place in Marmion Lagoon, 20 km north of Perth, Western Australia (32°S latitude) (Smale et al. 2011; de Bettignies et al. 2012a). This coastline is characterized by a series of successive high relief reef ridges (reef lines) running parallel to the shore, dissipating the hydrodynamic forces as waves approach the coast, creating a gradient in wave exposure (Phillips et al. 1997; Smale et al. 2011). This region is strongly influenced by westerly and south-westerly wind and swell-generated waves (Lemm et al. 1999) with prevalent storms in winter (waves >4 m, up to 8–9 m offshore). We investigated the range of water velocity experienced by *E. radiata* in the study region, particularly during storms in winter (Lemm et al. 1999), when maximum velocities are usually recorded and hence when morphological variation may be critical for survival. The instant water velocities were measured every 30 s at four reefs of different wave exposure in Marmion Lagoon. Measurements were carried out with gravitational data loggers (HOBO Pendant G, Onset Computer Corporation, Bourne, MA, USA) mounted on a 40-cm flexible aerial with blades (for technical details see 'H_2OMotionV1 design' in Evans and Abdo 2010). Prior to the deployment, the devices were calibrated in the field against an acoustic Doppler velocimeter (ADV, D. Thomson-CSIRO) to obtain the corresponding water velocity (m s^{-1}). The loggers were deployed for 1 week in winter (July 2010), a period that encompassed both general winter wave pattern and a significant storm (south-westerly swell), as indicated by a maximum 7 m wave height (averaged per hour) and 12–17 s wave period as measured by an offshore wave rider buoy. This event was similar to the frequent storms associated with mid-latitude depressions that occur in winter (>20 events per year, Lemm et al. 1999), and therefore, the range of velocities encompassed during this week is typical of what velocities kelp can experience in winter.

Kelp collection

Adult kelp thalli with thallus fully differentiated into complex laterals (stage 3 sporophytes, $N = 45$, Kirkman 1981) were collected from subtidal reefs (~8 m depth) between April and May 2009 (austral autumn) by carefully cutting immediately above the holdfast. To obtain a maximum range of morphotypes, the collections targeted kelps from Hamelin Bay (34°14′S; 115°01′E) and Marmion Lagoon (31°50′S; 115°42′E), two locations known to have morphologically distinct kelps (Wernberg et al. 2003a). The algae were kept moist during transport in an oxygenated cool box with ice packs and seawater, and were stored in situ in underwater cages for one night before undertaking drag measurements the following day.

Drag and water velocity measurements

Drag was measured while towing kelps behind a boat at known speeds in an experimental set-up similar to that used by Utter and Denny (1996) with *Macrocystis pyrifera* and Koehl (2000) with *Chondracanthus exasperatus*. Individual kelp thalli were tied to a non-flexible cord running through a metal pole and pulled through the water horizontally at a depth of about 1 m, a distance from the boat of 1.5 m on the side and 4 m downstream from the pole to avoid surface and wake effects generated by the boat and equipment. The cord was connected to a 5-kg, high precision, Pesola spring scale (Baar, Switzerland) to record maximum drag forces (drag pointer) encountered by the kelp during a 30-s run at relatively constant speed. Concurrently, water velocity was measured with a current velocity meter (model OSS-PC1, Hydrological Services Pty Ltd) placed 10 cm above the alga. For each thallus, the drag force was measured at four water velocity intervals (1–1.5, 1.5–2, 2–2.5 and 2.5–3 m s^{-1}), representative of velocities encountered by kelps in winter during high wave action (results from the HOBO loggers, Fig. 1). Speeds >3.0 m s^{-1} could not be reliably measured due to turbulence around the kelp produced by the set-up. This experiment was run inside ocean reef harbour 10 km north of Marmion Lagoon (Western Australia), protected by a rocky sea wall to minimize effects of wind and waves.

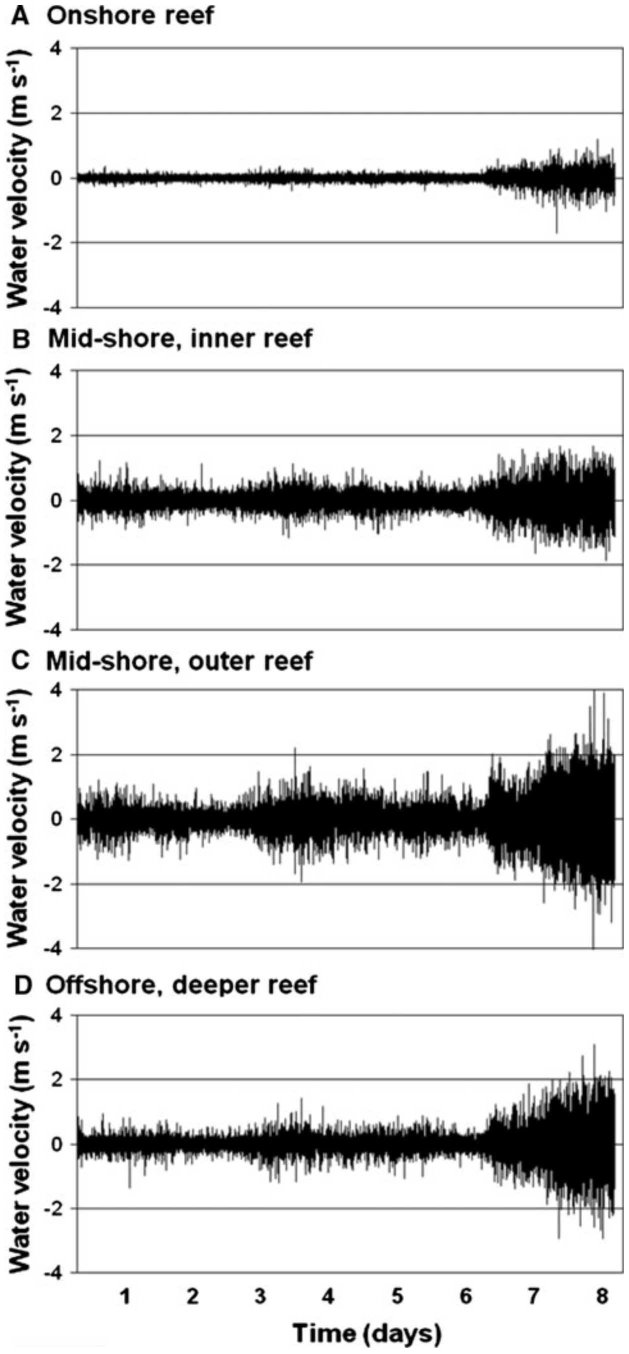

Fig. 1 Orbital water velocities recorded at four reefs over 8 days including a storm event, from 2 to 10 July 2010, using a 30-s sampling rate

Morphology

For each kelp thallus, 10 morphological characters describing the gross morphology were measured. An additional three derived area measures and two shape indices were calculated (Table 1, Wernberg et al. 2003a). Immediately after collection, the algae were weighed and a photo taken of each thallus by holding it upside down against a white background. The picture was analysed with *ImageJ 1.41* (*Image processing and Analysis in Java*) and calibrated against a known area. Three different measures of area were derived per thallus based on past drag studies on seaweed (Carrington 1990; Denny 1994; Wernberg 2005). Two measures were obtained by analysing the photography (planform area and frontal area), and the total area was obtained from a biomass–area relationship. Planform and frontal area (or profile area) are, respectively, the orthographic projection of the thallus on a plane either perpendicular or parallel to the direction of motion induced by the water current (= direction of the kelp held upside down). The frontal area was calculated as the circular cross-sectional area with the maximum thallus width as the diameter, obtained from the thallus photography. The planform area was calculated as the thallus area seen on the picture. Finally, the total area was obtained from the biomass (wet weight, WW) by applying WW:AREA from small batches of laterals and lamina of known areas (19.63 cm^2) for 25 plants (3 from laterals and 3 from lamina haphazardly taken from each thallus). Lamina and laterals accounted for 11.7 % (±2.95, $N = 25$) and 87.2 % (±3.12,

Table 1 Description of morphological characters, shape index and the procedures to measure or calculate them

Morphological characters	ID	Measurement
Primary morphology		
Total length (cm)	TL	Length of the thallus to the distal end of the frond (without stipe)
Thallus width (cm)	TW	Greatest width of the thallus when holding it upside down
Lamina length (cm)	LL	From where the stipe widens and flattens into the frond to the distal end of the central lamina
Lamina width (cm)	LW	Width measured at an arbitrarily selected place on the mid-1/3 of the central lamina
Lamina twist (count)	LT	Number of full rotations of the central lamina
Lateral density (number cm^{-1})	LAD	Density of secondary laterals (except were heavily eroded) protruding from the central lamina
Lateral length (cm)	LAL	Average length of 3 laterals arbitrarily selected from the mid-1/3 of the central lamina
Lateral width (cm)	LAW	Width of the selected (cf. lateral length) secondary lateral at its widest place
Lateral ramifications (count)	LAR	Number of ramifications for 3 consecutive laterals. Arbitrarily, from the mid-1/3 of the central lamina
Wet weight (g)	WW	Thallus wet weight after collection
Derived areas (cm^2)		
Total area	TA	Biomass converted to area by applying WW:AREA obtained from small batches of lateral and lamina.
Planform area	PA	Projected area of one side of an alga hold upside down by analysing pictures.
Frontal area	FrA	Orthographic projection of the thallus on a plane perpendicular to the direction of motion or frontal area.
Shape indexes		
Bushiness index	BI	Circumference (calculated with TW as diameter)/total Length
Flatness index	FI	Planform area$^{3/2}$/volume (volume for *E. radiata* thallus was calculated as the volume of 2 cones joint by their base when kelp held upside down)

$N = 25$) of thallus biomass, respectively, with mean biomasses per cm^2 of 0.20 g (lamina, ± 0.05, $N = 25$) and 0.10 g (laterals, ± 0.03, $N = 25$). Stipes accounted for only 1.1 % of the total biomass and were ignored. From these measures, the total area was calculated as:

$$\text{Total area } (\mathrm{cm}^2) = \frac{(0.1172 \times \mathrm{WW})}{0.2} + \frac{(0.8721 \times \mathrm{WW})}{0.1}, \qquad (1)$$

where WW is the total wet weight (g) of a thallus. The two shape indices were the bushiness index and the flatness index (BI and FI, Table 1). The BI, calculated as the circumference (with maximum thallus width as the diameter) to length ratio of the thallus, indicates how streamlined a kelp is (Begin and Scheibling 2003; D'Amours and Scheibling 2007), and the FI represents the degree to which a plant grows as a flat sheet (Gaylord 2000).

The drag equation

Drag is due to two components of an object: shape (form drag) and surface of the body (skin drag) (Vogel 1994). In biomechanical studies, drag is defined from the standard empirical drag equation (Vogel 1984; Denny 1995) as:

$$F_{\mathrm{drag}} = \frac{1}{2}\rho \times U^2 \times C_{\mathrm{drag}} \times A, \qquad (2)$$

where F_{drag} is the drag force (Newton), ρ the density of seawater (1,026 kg m^{-3}), U the water velocity (m s^{-1}), C_{drag} the drag coefficient (dimensionless) and A the 'object area' (m^2).

Data analysis

An ordination was performed for 45 thalli, each described by 15 morphological variables (Table 1) to verify that the kelps sampled did not cluster into similar morphological groups. The ordination was performed using a PCO based on a Euclidian distance matrix. To examine the impact of morphological variation on drag, morphological data were $\log_{10}$-transformed to obtain normalized multivariate data. Euclidian distance was used as the dissimilarity measure for drag measures. The distance-based linear models (DISTLM) routine, based on the $\mathrm{AIC_c}$ model selection criterion with a forward selection procedure (McArdle and Anderson 2001; Anderson 2003), was then used to examine the impact of algal morphology on drag. The selection criterion employed in this analysis was a modified version of the information criterion (AIC) (Akaike 1973), namely AIC_c, used where the number of samples (n) relative to predictor variables (q, the 14 morphological variables) is small (i.e. $n/q < 40$) (Burnham and Anderson 2002).

Results

In-situ orbital water velocity

During 1 week in winter (July 2010), the four reefs exhibited differences in orbital velocities, ranging from <1 m s^{-1} for the onshore reef to more than 3 m s^{-1} with few peaks reaching 4 m s^{-1} for the mid-shore outer reef (Fig. 1). While water velocity generally increased with distance of the reefs offshore, the most offshore site (Fig. 1d) did not show a higher velocity than the mid-shore outer reef (Fig. 1c), possibly due to differences in depth. The first three reefs had depths of 7–8 m, while the deeper offshore reef was at 10–11 m, therefore wave energy being more dissipated. A shift from general winter conditions to a storm period after 6 days of deployment was observed (Fig. 1). The loggers registered maximum orbital velocities of 3–4 m s^{-1} at the most exposed reef (Fig. 1c) and on average 1.5–2 m s^{-1} regardless of the reef (Fig. 1). Unfortunately, the memory capacity of the loggers was exceeded before the end of the storm, so it is possible that higher velocities may have occurred.

Morphological determinant of drag

Prior to analysing the morphological determinants to drag, the kelp collected were viewed with a PCO based on a Euclidian distance matrix according to their morphological attributes to explore their morphological variations. The first two axes of the PCO explained 64.9 % of the total variation inherent in the resemblance matrix and the thalli did not cluster into discrete groups (Fig. 2). The population of kelps (stage 3) was taken across different environments (different reefs, wave exposures and distances from shore) and was likely to approximate the maximum morphological variations occurring in situ. Drag forces increased as velocity increased with values (mean ± SD, N) of 16.43 ± 6.03 N ($N = 45$), 25.61 ± 7.81 N ($N = 45$), 34.98 ± 10.35 N ($N = 45$) and 46.70 ± 15.65 N ($N = 45$) for the respective classes of water velocities 1–1.5, 1.5–2, 2–2.5 and 2.5–3 m s^{-1}. All morphological parameters were included in the multivariate multiple regression model (forward DISTLM in PRIMER) except for thallus biomass (total area being a proxy for the biomass). The correlation of morphological variables with drag increased from 0.41–0.37 to 0.50–0.71 (r^2, Table 2) as velocity increased beyond 2 m s^{-1}, indicating a growing importance of morphological parameters at higher water velocity. At the lowest speed (1–1.5 m s^{-1}), thallus width characteristics, such as lamina width and thallus width, were determinant of drag, but not thallus area (Table 2). However, the drag at higher velocities was strongly related to change in total area (proxy of biomass) with an r^2 up to 0.59 for the model at high speed (2.5–3 m s^{-1}, Table 2). The increase in r^2, for the overall model at higher velocities, was explained by the increased ability of the total area to explain drag (r^2 increased from 0.26 to 0.59, Table 2), whereas addition of other morphological variables improved the model by only 10 % on average. Lamina width was an important parameter in the models at all speeds, though its contribution to explaining drag was greater at lower speed.

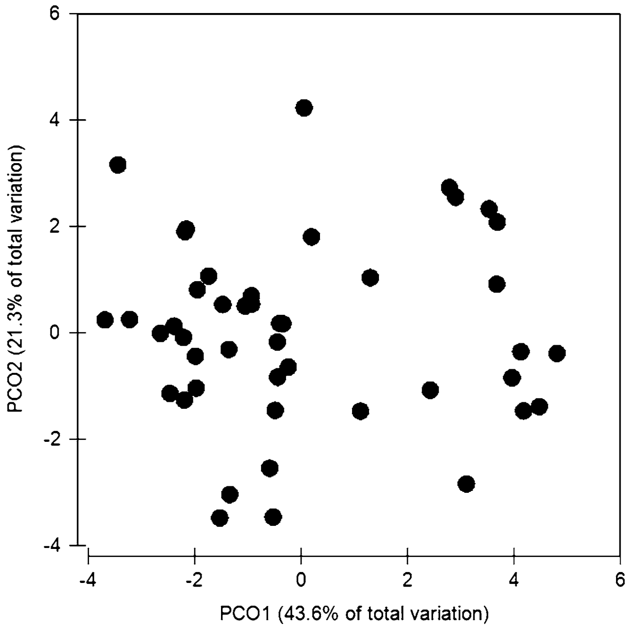

Fig. 2 Principal component ordination (PCO) of morphological variation (15 morphological characters) among *E. radiata* thalli ($N = 45$) used for drag measurement

Variation of C_{drag} with water velocity

According to our results, C_{drag} was estimated using the measure of total thallus area for the 'object area' (Eq. 2).The overall C_{drag} value and variance for the 45 kelps tested at the four velocities decreased with increasing water velocity following a negative power regression curve ($P < 0.001$, Fig. 3). However, the correlation coefficient was relatively low ($r^2 = 0.14$, Fig. 3). At low velocity

Table 2 Outputs from sequential tests of the multivariate analysis for a linear model using forward selection (DISTLM-Forward in PRIMER) at each water velocity class

Velocity (m s^{-1})	Model	AIC$_c$	SS (trace)	Pseudo-F	P_i	r^2
1–1.5	LW	134.9	518.7	20.4	0.0002	0.34
	LW + TW	132.9	100.3	4.3	0.04	0.41
1.5–2	TA	161.4	665.3	13.7	0.001	0.26
	TA + LW	157.2	282.2	6.65	0.01	0.37
2–2.5	TA	168.2	1915.3	30.2	0.0001	0.44
	TA + LW	166.1	253.6	4.4	0.04	0.50
2.5–3	TA	179.6	5458.1	51.3	0.0001	0.59
	TA + LAL	175.9	563.7	6.0	0.02	0.65
	TA + LAL + LW	171.2	565.7	7.1	0.01	0.71

All morphological variables (Table 1) were entered into the analysis

AIC$_c$ modified Akaike information criterion, SS (trace) portion of sum of squares related to the analysed predictor variable, r^2 percentage of variance explained by the variables selected in the model, P_i probability for the model. *TA* total area, *LW* lamina width, *TW* thallus width, *LAL* laterals length (see Table 1)

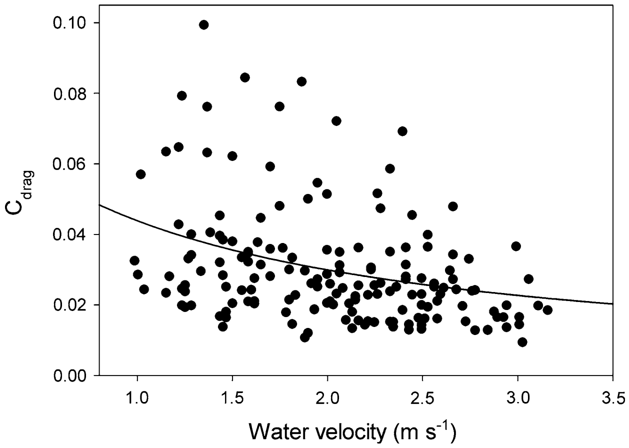

Fig. 3 Variation of drag coefficient (C_{drag}) with water velocity. Negative power regression curve displayed ($C_{\mathrm{drag}} = 0.041 \times$ water velocity$^{-0.634}$, $P < 0.001$, $r^2 = 0.14$, $N = 167$)

(1–1.5 m s^{-1}), C_{drag} values were highly variable ranging from 0.02 to 0.10 (0.037 ± 0.020, $N = 45$; mean and SD for C_{drag} between 1 and 1.5 m s^{-1}) converging to 0.024 (± 0.011, $N = 45$; mean and SD for C_{drag} between 2.5 and 3 m.s^{-1}, Fig. 3) as velocity increased. According to the regression equation ($C_{\mathrm{drag}} = 0.041 \times$ water velocity$^{-0.634}$, Fig. 3), C_{drag} values varied from 0.037 at 1–1.5 m s^{-1} to 0.022 at 2.5–3 m s^{-1}. During the storm monitored, the range of maximum water velocities was 2–3 m s^{-1} which resulted in an averaged C_{drag} of 0.025 (Figs. 1, 3).

Discussion

This study was the first worldwide to record continuously orbital water velocities generated by storm on temperate subtidal reef in situ. During the storm we monitored, kelp experienced orbital water velocities over 2 m s^{-1} (up to 3–4 m s^{-1}), comparable to the velocities we applied to kelp of different morphologies. Knowing the range of in situ velocities provided ecological content for the simulation of storm velocities on individual kelp thalli. Once kelp was subjected to these high water velocities, total thallus area or biomass became the main determinant of drag and not the morphological variation in shape. Variables related to the shape of the algae were important at low speeds only. These finding, together with the observed decrease in C_{drag} with speed, highlight the significant reconfiguration of the thallus occurring at high water velocity. This reconfiguration in high flow resulted more likely in the algae equally streamlined despite further increases in velocity, effectively decoupling hydrodynamic forces such as drag from algae shape.

The morphological determinants of drag, and their relationship with drag, varied with water velocity. At speeds that were low in the experiment, but in an ecological context are relatively high (1–1.5 m s^{-1}), the width of the lamina and thallus were the two most important variables explaining pressure drag, related to the form of the object. This is typically the case for algae with a flat, strap-like morphology, where width of the thallus is a crucial morphological parameter (Koehl and Alberte 1988), or for small bushy algae (*Codium fragile*), where the circumference to length ratio or BI drives changes in drag (D'Amours and Scheibling 2007). At higher velocities, the lamina width remained an important parameter in the model. This indicated that the lamina width may limit the potential of the thallus to reconfigure under high water velocities. The effect of this variable for *E. radiata* has been suggested previously by (Wernberg 2005) who found a trend of narrower lamina and laterals for kelps on exposed reefs. However, once the velocity reached

1.5 m s^{-1}, the main determinant of drag became the total area of the thallus or biomass. Milligan and De Wreede (2004) found similar results comparing morphotypes of an intertidal alga, *Hedophyllum sessile*, and showed that morphological variations in shape did not reduce the drag stress when water velocity reached 4 m s^{-1}. In theory, two forms of drag can be distinguished (Vogel 1994): drag caused by build-up of pressure in front of the body and a decrease in pressure behind the body, called *pressure drag* or *form drag*; and the viscous resistance of the fluid along the surface of the body, called *skin drag* or *friction drag*. The results indicated that friction and pressure drag could act together in complex algae like *E. radiata*, but their relative importance changes with water velocity. At low speeds, the lamina and thallus width best explained drag (pressure drag), but as water velocity increased, the total area (combining both drags) was better related to drag. Indeed, the ability of flexible organisms to reconfigure reduces the size of the wake downstream, thereby reducing form drag at high flow (Carrington 1990; Koehl 2000).

The decrease in the drag coefficient with increasing velocity is consistent with the findings for drag force and corresponds to a reconfiguration of the algae to a more streamlined and compact shape (Koehl 1984; Koehl and Alberte 1988; Gaylord et al. 1994; Denny and Gaylord 2002). This implies that kelp morphology changes with the flow, and therefore, morphological determinant of drag must vary with water velocity (what we found). Similar to other studies, C_{drag} tends to reach an asymptote at higher velocities, and the effects of shape change were greatly reduced (Carrington 1990; Gaylord et al. 1994; Bell 1999; Boller and Carrington 2006). This can be explained by the flexibility of algae due to their relatively simple shape and the compliance of their materials that enables algae to reconfigure in rapid steady flows. This extreme reconfiguration in high flows can result in decoupling of hydrodynamic forces such that drag becomes relatively independent of the apparent differences of algae shape (Denny and Gaylord 2002). Past studies demonstrated similar results of converging C_{drag} for different morphotypes of a species (*Pachydictyon coriaceum*, Haring and Carpenter 2007) and for different species (Carrington 1990). Although the drag coefficient can be calculated from different measures of thallus areas (Carrington 1990; Denny 1994; Wernberg 2005), the value obtained for C_{drag} (0.025) using the total area in our study was very similar to drag coefficients for several kelps under high flow regime: 0.01–0.05 (Koehl 2000; Kawamata 2001; Thomsen 2004).

The simulated unidirectional steady flow used in our experiments was a simplification of the oscillatory motion that occurs under wave action. Because waves generate orbital water flow, the reorientation of the plant and its ability to 'go with the flow' is likely to more efficiently reduce hydrodynamic forces (acceleration forces) than 'drag reducing shape'. Indeed, Wernberg and Vanderklift (2010) showed that morphological characters of *E. radiata*, associated with overall size, increased with increasing wave exposure. This could be an adaptation to follow the orbital flow, preventing the thallus being stretched out fully before the flow reverses, and reducing the forces experienced (Denny 1998; Koehl 1999). However, the combination of long wave periods during storm (~13–17 s, http://www.dpi.wa.gov.au and Lemm et al. 1999) and the relative small size of *E. radiata* (<1 m, Wernberg and Vanderklift 2010) should always result in the kelp being totally stretched out and experiencing the total force of the waves (Gaylord et al. 1994; Koehl 1999). Further investigation is needed to test the reciprocal impact of morphology on hydrodynamic forces via this strategy of 'going with the flow'.

These results confirm the importance of the object area as a determinant of drag, principally at high speeds, and the importance of other morphological variables related to the width, which probably limits the compaction of the object at lower speed. However, these morphological variables only had a minor effect on drag and C_{drag} converged at water velocities characteristic of storms due to the algae being equally streamlined at these higher velocities. Consequently, drag is decoupled from the shape and other morphological variables of the thallus, with the exception of total area, a function of biomass. Given this, the only way of minimizing drag forces at storm velocities is by a reduction in thallus area (biomass) and not by modification of thallus shape. Along the Western Australian coastline, storms associated with mid-latitude depression are common in winter (Lemm et al. 1999), and generally, algal dislodgment occurs during such severe storms, which generate high water velocities (Seymour et al. 1989; Dayton et al. 1992; Blanchette 1997). However, the temporal growth–erosion dynamic and the resulting decrease in individual kelp biomass (i.e. total area) for *E. radiata* in autumn–winter (Kirkman 1989; de Bettignies et al. 2012b) will minimize the drag force and might offset the increase in water velocities during the storms and the risk of dislodgement. Ultimately, the survival of *E. radiata* will depend of the balance between the drag force (as the main hydrodynamic force) and the force required to break or dislodge the algae (break force), related to its material properties and attachment to the substrate.

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