Botanica Marina 47 (2004): 454–460 © 2004 by Walter de Gruyter • Berlin • New York. DOI 10.1515/BOT.2004.068

The effect of thallus size, life stage, aggregation, wave exposure and substratum conditions on the forces required to break or dislodge the small kelp *Ecklonia radiata*

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Abstract

Canopy removal by storms is a primary cause of mortality for the small kelp *Ecklonia radiata* in temperate Australasia. We simulated hydrodynamic drag from storms with *in situ* pull-tests to determine whether thallus size, life stage, aggregation, wave exposure and substratum affect the canopy removal process. A total of 466 individuals were pulled off 20 rocky reefs at 8–10 m depth in southwestern Australia. The majority (71%) of thalli dislodged at the rock implying that the canopy removal process in southwestern Australia is a substratum-controlled process. Dislodgment bared clean substratum where re-invasion by propagules or encroachment would be necessary to fill up the gaps. Maximum break forces (150–250 N) were found for large late stage kelps and kelp aggregates from wave exposed sandstone and granite reefs, and minimum values (25–100 N) for small juveniles and solitary kelps from protected limestone reefs. By applying size and break force data to the drag equation, water velocities required to break or dislodge *E. radiata* were calculated to 2–5 ms^{-1} for large kelps. These velocities are frequently encountered in wave-exposed shallow subtidal habitats, suggesting that thallus size is limited by the hydrodynamic environment.

Keywords: break force; break place; canopy removal; dislodgment; disturbance; *Ecklonia*; pruning.

Introduction

Canopies of large macroalgae influence their surrounding environment and, when they are removed, there are subsequent changes to light levels, water motion, sediment deposition and thallus abrasion in the understorey (Eckman et al. 1989, Kennelly 1989, Melville and Connell 2001, Connell 2003). These changes to the physical environment influence the understorey inhabitants (Melville and Connell 2001, Connell 2003, Toohey et al. 2004) and, consequently, canopy removal is a driving process in the organization of many rocky reef assemblages. Hence, a mechanistic understanding of the canopy removal process could facilitate a broader understanding of population and community dynamics in habitats dominated by macroalgal canopies.

Wave exposure is a major cause of canopy removal worldwide (Kennelly 1987, Seymour et al. 1989, Dayton et al. 1992, Blanchette 1997, Markel and DeWreede 1998). Canopy removal occurs either as dislodgment where entire algae are broken off at the substratum, or by pruning where parts of thalli are torn off. Pruning of many laminarian algae (kelps) will lead to complete canopy removal if the damage includes the lower part of the thallus where the primary meristem is located (Kennelly 1987, Cole and Syms 1999). Whether the canopy is removed by dislodgment, or by different degrees of pruning may have implications for the succession of species colonizing the newly formed gap (Kennelly 1987), because dislodgment generates relatively clean substratum whereas pruning leaves the holdfast and substratum with associated propagules and macroscopic animal and algal assemblages, intact (Sousa 1985). We believe that pruning and dislodgment play major roles in the population structure and survivorship of thalli of the kelp-*Ecklonia radiata* (C. Ag.) J. Agardh.

The process of canopy removal can be simulated and quantified by a biomechanical pull-test where the force required to break an alga (the break force) and the corresponding breaking point on the thallus (the break place) are determined (Hawes and Smith 1995, Shaughnessy et al. 1996). Factors that may affect break force include thallus size (Carrington 1990, Shaughnessy and DeWreede 2001, Milligan and DeWreede 2004), life stage (Milligan and DeWreede 2000), aggregation (Holbrook et al. 1991), wave exposure (Milligan and DeWreede 2000, Kawamata 2001) and substratum type (Barnes and Topinka 1969, Malm et al. 2003). The relative importance of these factors is, however, unknown for most macroalgae including the small kelp *Ecklonia radiata*, a dominant canopy-former on subtidal temperate rocky reefs of South Africa, Australia and New Zealand (Bolton and Anderson 1994, Wernberg et al. 2003b). We tested the hypotheses that thallus size, life stage, aggregation, wave exposure and substratum affect break force and break place in this species.

Material and methods

Measurement of break force and break place

Samples were collected at 8–10 m depth (except site 20 at 1 m depth) between October 2000 and February 2001

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Table 1 *Ecklonia radiata*: site characteristics and number of replicate thalli.

Site	Locality	n_1	n_2	Substratum	# Reefs	Comments
1	Albany 1	16	15	Granite	0	Low relief, flat terrace
2	Albany 2	14	14	Granite	1	Behind an island, on round boulders
3	Hamelin 1	17	14	Limestone	1	High relief
4	Hamelin 2	19	15	Granite	0	High relief
5	Hamelin 3	18	18	Limestone	2	High relief
6	Jurien 1	20	20	Limestone	2	Low relief
7	Jurien 4	14	14	Limestone	0	Intermediate relief
8	Kalbarri 1	19	19	Sandstone	1	Low relief, low slope
9	Kalbarri 3	14	13	Sandstone	1	Low relief, low slope
10	Mandurah 1	19	17	Limestone	2	Low relief, low slope
11	Mandurah 2	9	7	Limestone	2	Low relief, low slope
12	Marmion 1	27	22	Limestone	0	Intermediate relief
13	Marmion 2	26	25	Limestone	0	Intermediate relief
14	Marmion 3	21	20	Limestone	0	Intermediate relief
15	Marmion 4	12	12	Limestone	1	Intermediate relief
16	Marmion 5	130	120	Limestone	1	Low relief, low slope
17	Marmion 6	21	17	Limestone	2	Low relief, low slope
18	Marmion 7	19	14	Limestone	2	Low relief, low slope
19	Marmion 8	18	16	Limestone	2	Low relief, low slope
20	Marmion 9	13	13	Limestone	3	Inside harbor, on jetty boulders

See Wernberg et al. (2003a) for geographic coordinates of localities. The within-locality identifier corresponds to rocky reefs within a locality, separated by a minimum of 1 km. A total of 466 kelp thalli were sampled for break place and break force (n_1), but because some individuals could not be brought ashore, kelp size was only measured on 425 individuals (n_2). # Reefs indicate how many wave-attenuating rocky reefs were in front of the reef sampled.

from 20 rocky reefs within six localities in southwestern Australia (Table 1). Within localities, reefs were separated by a minimum of 1 km. Break force and break place were measured *in situ* on haphazardly selected *Ecklonia radiata* individuals. A strip of nylon webbing was tied around the mid-thallus and pulled steadily at a 30° angle to the substratum using a 20 or 50 kg (±0.3% of maximum extension) Pesola spring scale (Baar, Switzerland) for 5–10 s until breakage. The measurement was discarded if the breaking point was near the webbing. The tested specimens were tagged and brought to the shore for wet weight determination. Break place was classified as one of five categories, ordered from the substratum to the webbing: 1) rock, 2) holdfast and holdfast-stipe junction, 3) stipe, 4) stipe-thallus junction including the lower thallus with the primary meristem, and 5) the lower thallus from above the meristem to the webbing. Category one corresponds to our definition of dislodgment, whereas categories 2–5 correspond to progressively decreasing levels of pruning intensities. Kelp survival is only possible if the breaking point is at category five (Kennelly 1987, Cole and Syms 1999). Life stage and degree of aggregation (number of fused holdfasts) were recorded. Life stages followed Kirkman (1981): stage 1 (S1, 6.5–27 cm), the small recruit stage where the lamina is undifferentiated, stage 2 (S2, 19–34 cm), the old recruit stage where the lamina starts to develop primary laterals and stage 3 (S3, >30 cm), the adult stage where the thallus becomes fully differentiated into complex laterals. A fourth stage (S2b), the young adult stage, intermediate between stages 2 and 3 was also included.

Some authors pull horizontally relative to the substratum to simulate drag forces more realistically (e.g., Hawes and Smith 1995, Blanchette 1997), but a preliminary test between pulling angles of 0° or 30° showed no significant differences for stage 2 and 3 individuals for either break force (t-tests: S3, $p=0.51$, $n=52$; S2, $p=0.51$, $n=26$) or break place (χ^2-tests: S3, $p=0.27$, $n=52$; S2, $p=0.98$, $n=26$), and the 30° pull-angle was chosen as it was easier to work with in the swell-dominated environment. We also recorded the site-specific substratum type (limestone, granite or sandstone) and estimated the number of successive wave-attenuating rocky reefs in front of each site from charts to get a relative measure of wave exposure (Friedland and Denny 1995). Within southwestern Australia such reef structures have previously been shown to attenuate wave energy (Phillips et al. 1997).

Data analysis

Because each kelp individual has a unique size, a regression approach was used to test relationships between thallus size, break force and break place. Size vs. break force was fitted with reduced major axis linear regression on Log-transformed data. To simplify the test of thallus size vs. break place, the original five categories were pooled into ecologically relevant dichotomous groups: below vs. above the meristem (=canopy removal vs. recovery) and rock vs. kelp (=absence vs. presence of holdfast-associated organisms) and tested with logistic regression. The effect of life stage on thallus size and break force was tested with ANOVA. Although thallus size and life stage correlate (Kirkman 1981, Larkum 1986), the former continuous variable is related to age and growth conditions (Sjøtun and Fredriksen 1995), whereas the latter categorical variable is identified from specific morphological characteristics (Kirkman 1981). The effect of life stage on break place was tested with a χ^2-test. Similar tests were used to test the effect of aggregation, wave exposure and substratum on thallus size, break force (ANOVAs) and break place (χ^2). All individuals were pooled as replicates across sites for all individual-based tests (Table 2). In the test of substratum type, the five

Table 2 *Ecklonia radiata*: test factors, levels, and data pooling.

Test factors	Test levels	Data pooling procedure
Size	0–3000 g WW	All sites (all individuals)
Life stage	S1 vs. S2, vs. S2b vs. S3	Marmion, Hamelin, Albany, Kalbarri, Mandurah (solitary individuals)
Aggregation	Solitary vs. aggregates	Marmion (S3 individuals)
Wave exposure	4 exposed vs. 4 protected sites	Albany 1 vs. 2, Jurien 1 vs. 4, Hamelin 2 vs. 3, Marmion 1 vs. 8 (solitary S3 individuals)
Substratum type	5 hard vs. 5 soft sites.	Albany 1, 2, Hamelin 2 and Kalbarri 1, 2 vs. Jurien 1, Hamelin 3, Marmion 5, 8, Mandurah 1 (solitary S3 individuals)

The response variables for the test factor “size” were “break place” and “break force”. In addition to these, the response variable “thallus size” was added for the remaining four test factors. Data subsets were selected by random tables to ensure balanced sample designs.

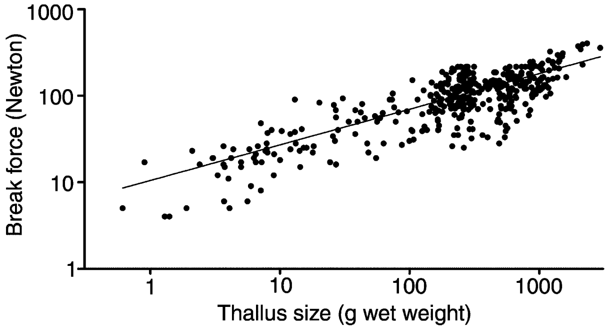

Figure 1 *Ecklonia radiata*: kelp size vs. break force: Log $F_{break}=0.95+0.43*\text{Log WW}$, $p<0.001$, $r^2=0.68$, $n=425$.
There were no significant correlations between break place and size (Table 3).

granite and sandstone sites (Table 1) were grouped as “hard” substratum and tested against five randomly selected limestone sites (Table 2) grouped as “soft” substratum. It should be emphasized that each test was designed to include individuals that only differed with respect to the single test factor of interest, e.g., the wave exposure test only included solitary adult individuals, and the aggregation test only included life stage 3 individuals of similar wave exposure and substratum conditions (Table 2). All ANOVAs and χ^2-tests were conducted on data sets balanced by randomly deleting replicates from groups with replicate surplus. Life stage, aggregation, wave exposure and substratum were treated as fixed factors, and sites and localities as random factors. Data for ANOVA were checked for homogeneity of variances with Cochran’s C-test and transformed if $p<0.05$. To reduce the number of categories with low expected frequency of occurrence, all χ^2-tests were conducted on break categories pooled into three groups: rock, kelp below the meristem or kelp above the meristem. Because each test constituted an independent test of a separate hypothesis about a specific biomechanical property, the α-values were not adjusted for multiple testing.

Results

There was a significant positive correlation between thallus size and break force (Figure 1), but no significant relationships between thallus size and break place (Table 3). The majority (71%) of *Ecklonia radiata* thalli broke at the rock followed in frequency by the stipe-thallus junction, thallus, holdfast, and stipe (Figure 2D). The life-stage based results were consistent with the size-based results in that late-stage kelps were significantly larger (Figure 2A, Table 4) and more strongly attached (Figure 2B, Table 4) than at early stages. The different life stages broke the same places (Figure 2D, Table 3) although there was a tendency for early life stages to have a higher proportion of breakage at the rock with S1>S2>S2b>S3 (Figure 2D). Kelp aggregates were significantly larger (Figure 2A, Table 4) and more strongly attached (Figure 2B, Table 4) than solitary kelps. Although non-significant (Table 3), solitary kelps had a tendency to break more often at the stipe-thallus junction and thallus, and less often at the rock surface than kelp aggregates. Kelps from exposed rocky reefs were similar in size to kelps from protected reefs (Figure 2A, Table 4), but they were significantly more strongly attached (Figure 2B, Table 4). Also, kelps from exposed reefs broke significantly less at the rock but more often above the meristem (Figure 2D, Table 3). Kelps on hard substratum were significantly smaller than kelps on soft substratum (Figure 2A, Table 4). In addition to being smaller, the kelps on hard substratum were significantly more strongly attached (Figure 2B, Table 4) than kelps on soft substratum. Finally, kelps on hard substra-

Table 3 *Ecklonia radiata*: χ^2-tests for effects of thallus size (logistic regressions), life stage, aggregation, wave exposure and substratum on break place.

Test number and factor	χ^2	n	df	p
Size (below-above meristem)	419.17	425	422	0.532
Size (rock surface-kelp)	424.23	425	422	0.464
Life stage	3.86	96	6	0.696
Aggregation	4.61	38	2	0.099
Wave exposure	33.16	112	2	<0.001
Substratum	12.03	130	2	0.002

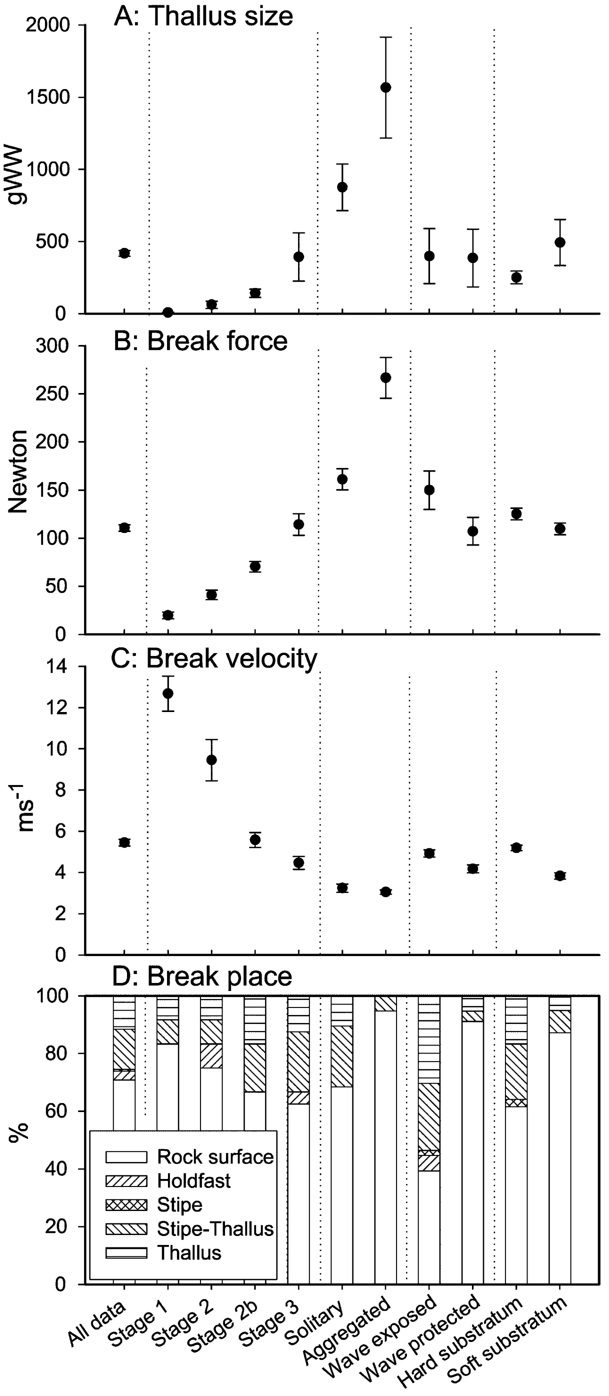

Figure 2 *Ecklonia radiata*: kelp size (A), break force (B), break velocity (C) and break place (D) for all data pooled and for different life stages, levels of aggregation and wave exposure, and substratum types (mean±SE, n from left=466, 24, 24, 24, 24, 19, 19, 56, 56, 65 and 65).
All tests were significant ($p<0.05$), except wave exposed vs. protected break sizes and stage 1 vs. stage 3 break places.

tum broke less frequently at the rock but more often at the stipe-thallus junction and thallus (Figure 2D, Table 4).

Discussion

Ecklonia radiata responded to our pull-tests in a predictable way: large, late life-stage individuals and aggregates from wave-exposed sites and from granite and sandstone reefs (hard substratum) had higher break forces than small, early-life stage and solitary kelps from protected sites and from limestone reefs (soft substratum).

Thallus size

Stage 3 and kelp aggregates were larger than stage 1 and solitary kelps, as expected from a simple allometric growth-model (Kirkman 1981). Kelps from wave-exposed sites had biomasses similar to those of thalli from protected sites, as observed by Molloy and Bolton (1996) and Kawamata (2001), but different from other studies that report smaller algae at exposed sites because of frequent pruning (Blanchette 1997, Pratt and Johnson 2002). Kelps on granite and sandstone reefs were small compared to those on limestone reefs, but as there is no *a priori* reason why kelps should grow slower on granite or sandstone than on limestone, this probably reflects the fact that kelps on hard substratum are pruned more intensely. Thus, because kelps have a strong attachment on granite and sandstone reefs, they break more often above the meristem, thereby surviving and resulting in small individuals. This is consistent with the break place data (see later).

Break force

Ecklonia radiata was slightly more strongly attached (110–150 N, this study) compared to the smaller kelps *Hedophyllum sessile* (C. Agardh) Setchell (80–120 N, Milligan and DeWreede 2000) and *Egregia menziesii* (Turner) Aresch. (90–130 N, Friedland and Denny 1995), but weaker than the larger algae *Laminaria schinzii* Foslie (490–580 N, Molloy and Bolton 1996) and *Durvillaea antartica* (Chamisso) Hariet (1160 N, Smith and Bayliss-Smith 1998), suggesting a general relationship between thallus size and attachment strength. In concordance with other studies (Carrington 1990, Milligan and DeWreede 2000, Kawamata 2001, Duggins et al. 2004), large and late-stage individuals and aggregates of *Ecklonia radiata* thalli were more strongly attached than early life stage individuals (Table 2), likely because they have larger holdfasts and stipes (Carrington 1990, Dudgeon and Johnson 1992, Duggins et al. 2004). *E. radiata* thalli from wave-exposed sites were more strongly attached than individuals from protected sites, as observed for many other macroalgae (Jackelman and Bolton 1990, Friedland and Denny 1995, Kawamata 2000, Milligan and DeWreede 2000, Kawamata 2001, Blanchette et al. 2002, Duggins et al. 2004). However, numerous other studies have also found no effect of wave-exposure (Norton 1986, Johnson and Koehl 1994, Molloy and Bolton 1996, Van Tamelen and Stekoll 1996, Pratt and Johnson 2002, Malm et al. 2003). Among these studies, only ours and that of Jackelman and Bolton (1990) replicate wave-exposure at the site-level. The observed pattern can reflect either that weakly attached kelps are dislodged disproportionately from exposed rocky reefs, thereby shifting the distribution of breaking forces to higher values, or that kelps on exposed reefs produce larger holdfasts, although the latter does not appear to be the case (Wernberg and Thomsen personal observation). Also, *E. radiata* was more strongly attached to hard than soft sub-

Table 4 *Ecklonia radiata*: ANOVA tests for life stage, aggregation, wave exposure and substratum on thallus size and break force.

		Thallus size			Break force		
Source of variation	df	MS	F	p	MS	F	p
Life stage	3	5.03[a]	194.3	<0.001	30.91[b]	106.1	<0.001
Error	92	0.026			0.291		
Aggregation	1	891.9[d]	15.8	<0.001	0.512[a]	13.1	0.001
Error	36	56.5			0.039		
Wave exposure	1	0.002[c]	0.1	0.741	531.6	31.6	<0.001
Site (wave exposure)	6	0.646	37.6	<0.001	87.55	5.2	<0.001
Error	104	0.017			16.81		
Substratum	1	1914007[d]	112.0	<0.001	77.849	4.3	0.039
Site (substratum)	8	512175	23.0	<0.001	122.94	6.9	<0.001
Error	120	17094			17.94		

a: fourth root transformed, b: square root transformed, c: Log-transformed, d: could not be transformed to homogeneity (Cochran's C-test, p>0.05), thus not transformed. In the latter case, inspection of box plots did not reveal any exceptionally large variances and because of the balanced and relatively large sample design is considered a robust result (Underwood 1997).

stratum, as found with other algae (Barnes and Topinka 1969, Milligan and DeWreede 2000, Malm et al. 2003). The strength of the substratum is not a limiting factor on granite and some sandstone, thus the process of canopy removal switches from a substratum-controlled process on limestone (how strong is the substratum?) to an organism-controlled process on granite and sandstone (how strong are the different parts of the kelp?).

Break place

The majority of *Ecklonia radiata* thalli became dislodged at the reef rock level where the rock gave in. This differs from several other macroalgae that typically break at the stipe or holdfast-stipe junction (Carrington 1990, Shaughnessy et al. 1996, Duggins et al. 2001), and our observation suggests that the hardness of the limestone reefs in southwestern Australia is the limiting factor in resisting dislodgment, not the attachment capability of kelp holdfasts. There was no significant relationship between thallus size and break place, although there was a trend for a consistent decrease in the proportion of kelps that broke at the rock surface with increasing life stages. This could reflect the fact that early life stages with their small size and simple (low drag) morphology are not limited by weaknesses in the substratum to the same extent as later life stages. Hence, with increasing life stage, size, and drag, individuals attached to weak patches in the rock are selectively removed so that older individuals remaining in strong spots are more likely to break where the tissue is weak (e.g., meristem). In addition, older individuals may accumulate fractures and scars from abrasion, scouring, or grazers (Denny et al. 1989, Duggins et al. 2001) or experience tissue fatigue (Carrington 1990), increasing the relative weakness of the thallus. For example, Duggins et al. (2001) found that break force was lowered and more stipe-breakage observed (as opposed to holdfast breakage) in the presence of the grazing mollusc *Lacuna vincta* (Montagu). We did look for grazing scars and other potentially weakening marks but rarely found any. Similarly, aggregation did not have a significant effect on break place, but tended to increase the likelihood of dislodgment at the rock, suggesting that the strength of individual holdfasts is not additive when they fuse into aggregates. Kelps from wave exposed sites broke less often at the rock but more often in the thallus compared to kelps from protected sites. This suggest that the rocky reef is harder at exposed sites, for example because of the selective removal of soft parts of substratum over millennia, or that the kelp tissues are weaker, or that holdfasts are relatively larger or stronger at exposed sites. Finally, kelps on limestone reefs had a higher frequency of rock-breakage compared to kelps on sandstone and granite. When kelps on hard substratum broke around the holdfast, substratum was not removed, whereas dislodgment on limestone reefs created obvious erosion [pieces of broken rock remained attached to the holdfast (unpublished data, Wood 1980)]. Similar algal-induced erosion has been observed on barnacle shells (Barnes and Topinka 1969), coralline and encrusting algae (Milligan and DeWreede 2000) and basaltic rocks (Smith and Bayliss-Smith 1998). The breaking of the limestone reefs was likely facilitated by limestone-boring polychaetes, molluscs and algal haptera (Wood 1980).

Perspective: calculation of break velocities

Dislodgment or pruning depends on the balance between break forces and hydrodynamic drag forces from waves and currents. Acceleration forces, as a first approximation, can be ignored for flexible seaweeds (Hawes and Smith 1995, Bell 1999, Gaylord 2000, Pratt and Johnson 2002). The drag equation relates water velocity to drag force and by inserting break forces it is possible to calculate the theoretical water velocity required to break or dislodge a macroalga:

$$\text{break velocity}=[(2\times\text{break force})/(\text{drag coefficient}\times\text{planform area}\times\text{seawater density})]^{0.5}$$

(Denny 1995). These break velocities can be interpreted as susceptibility to breakage during hydrodynamic peak events such as storms, and may provide a tool for predicting the outcome of a disturbance event (Denny 1995). To estimate *Ecklonia radiata* break velocities, we applied our size-specific break force data to the drag equation (Figure 2C). Wet weights were converted to planform area from life-stage specific regressions obtained from kelps collected in the Perth area ($r^2>0.90$, $p<0.001$, $n_{S1}=20$,

n_{S2}=13, n_{S3}=35). The density of seawater was set to 1026 kg m^{-3} (10°C) and the drag coefficient to 0.03, being the middle of the 0.01–0.05 interval into which drag coefficients for several kelps converge under high flow regimes [review by Koehl (2000) and data from Kawamata (2001)]. It should be emphasized that these break velocities are estimates only and that they should be further refined by applying size, form and flow specific drag coefficients, and tested using a combination of wave force measurements and tagging experiments. A simple linear regression showed a negative Log-relationship between kelp wet weight and break velocity (Log break velocity (ms^{-1})=1.31–0.27*Log wet weight (g), r=-0.86, n=425). Using this equation, break velocities were estimated to be 10–25 ms^{-1} for small recruits and 2–5 ms^{-1} for adult kelps, i.e., the advantage of a low drag associated with a small thallus clearly outweighs the disadvantages of a weak attachment. Water velocities of 2–5 ms^{-1} are regularly encountered in shallow wave-exposed subtidal habitats (Gaylord et al. 1994, Denny 1995, Wernberg-Moeller 2002) and the calculated break velocities thus suggest that wave dislodgment is unlikely to be a major cause of recruit mortality whereas hydrodynamic forces probably are the primary cause of mortality in adult *E. radiata*, particularly in light of the low abundances of large herbivorous invertebrates in southwestern Australia (Fowler-Walker and Connell 2002, Vanderklift and Kendrick 2004). This supports the general hypothesis that the hydrodynamic environment sets an upper limit to size in wave-swept habitats (Carrington 1990, Gaylord et al. 1994, Denny 1995).

Acknowledgements

This research was supported by a grant from the Danish Research Academy to MST.

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Received 2 August, 2004; accepted 11 November, 2004