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Miniview: What affects the forces required to break or dislodge macroalgae?

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The forces required to break or dislodge benthic macroalgae can be linked to many important ecological processes such as survival, transport and dispersal, and it is, therefore, important to understand what factors affect these forces. We review existing studies, using simple vote-counting, to establish what ecological factors have been found to influence macroalgal break forces. We also used the compiled information to test for the existence of a general allometric relationship between thallus area and break force. We found 30 studies reporting break forces for 27 species of macroalgae from 118 populations. Species within the orders Laminariales, Fucales and Gigartinales were well studied whereas other orders had been neglected. Two-thirds of all studies were from rocky intertidal habitats and two-thirds were from North American coastlines. The most frequently tested ecological factor was wave exposure (14 studies with 7 significant effects). Other factors that were found to affect break force significantly in at least one study included time of sampling, thallus size, substratum and species. Generally, most factors had been addressed only a few times, emphasizing a need for further study. We found a highly significant positive relationship between thallus size and break force across a wide range of species and ecological conditions, providing evidence that size alone is an important determinant of macroalgal break force. To strengthen inferences and ensure that meta-analyses can be conducted, we suggest that future studies (i) use nested replication in space and time, (ii) include taxa and regions that have not been studied in detail, and (iii) report, as a minimum, corresponding information on break forces, thallus sizes, substratum type, wave exposure and time of sampling.

Key words: macroalgae, biomechanics, break force, dislodgment

Introduction

Dislodgment and breakage caused by waves and currents is one of the most important processes determining the survival of sessile organisms in marine environments (Lewis, 1964; Jones & Demetropoulus, 1968; Koehl & Wainwright, 1977; Norton, 1991; Denny, 1995). Differences in susceptibility to dislodgment and breakage cause predictable patterns in the distribution of biota, which traditionally have been summarized in biological wave-exposure classification schemes (Ballantine, 1961; Lewis, 1964). More recent approaches, however, separate the biological adaptation and distribution data from the hydrodynamic forces (Bell & Denny, 1994; Denny, 1994). In particular, Denny and co-workers (e.g. Denny, 1983, 1987, 1988, 1994; Denny *et al.*, 1985, 1997; Gaylord *et al.*, 1994; Gaylord & Denny, 1997) have strongly advocated a mechanistic approach to predicting dislodgment and breakage of wave-swept organisms by comparing the ambient hydrodynamic forces and the forces actually experienced by the organisms to the forces required to break these organisms. Nevertheless, Denny (1995, p. 398) concluded that, ‘‘our current lack of knowledge regarding the strength of organisms poses a potential impediment to widespread application of the method’’. Over a couple of decades, several studies have investigated the attachment characteristics of macroalgae. Yet, no one has compiled this data and attempted to assess the current state of knowledge, and information on macroalgal break forces appears fragmented and scattered. Consequently, our first objective was to review the empirical literature in order to identify what ecological factors have been investigated and found to affect the break forces of macroalgae. Although many environmental factors are likely to be important, thallus size has been suggested to be a fundamental factor scaling break forces (Gaylord *et al.*, 1994; Denny, 1995). Our second objective

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was, therefore, to use the compiled literature to test for the existence of a general allometric relationship between thallus size and break force.

Material and methods

Literature was found by entering key words relating to break force, attachment strength, dislodgment, macroalgal biomechanics, and tenancy distributions into the 'Current Contents' search engine. Older literature was found by back-tracking from more recent papers. Test factors and statistical results were recorded for each study (Table 1). A population – the fundamental unit for our test for an allometric relationship between break force and thallus size – was defined irrespective of taxonomy as an independent group of specimens sampled at a specific time and place. Mean break force and corresponding mean thallus size (area) was estimated for each population from tables, figures, text or published allometric relationships (cf. Appendices 1 and 2). The emphasis of our review was on data from *in situ* pull-tests – usually performed by wrapping a piece of webbing or string around the alga and pulling horizontally relative to the substratum with a spring scale until breakage – because these tests reflect real dislodgment and break processes well (Carrington, 1990; Hawes & Smith, 1995; Bell, 1999). Some stipe-extension

Table 1. Details of test factors and results from studies on macroalgal break forces. The three numbers under experimental design refer, respectively, to the number of sampled localities (sample areas separated by more than ca. 10 km), sites (sample areas separated by less than ca. 10 km), and sample times. Break force (N) and thallus size (m^2) for each population (group of specimens sampled at a specific time and place) can be found in Appendices 1 and 2.

Study no.	Reference	Experimental design	Species	Test factor ('+' = $p < 0.05$; '–' = $p > 0.05$)
1	Barnes & Topinka (1969)	1,1,1	*Fucus vesiculosus*	Substratum (–)[a]
2	Vogel & Loudon (1985)	1,1,1	*Halosaccion glandiforme*	None
3	Norton (1986)	1,1,1	*Fucus vesiculosus*, *Ascophyllum nodosum*	Wave exposure (–), Species (–)
4	Carrington (1990)	1,3,1	*Mastocarpus papillatus*	Thallus size (–)
5	Jackelman & Bolton (1990)	2,3,1	*Gigartina radula*	Wave exposure (+)
6	Holbrook *et al.* (1991)	1,2,3	*Postelsia palmaeformis*	Aggregation (–)
7	Dudgeon & Johnson (1992)	1,1,1	*Chondrus crispus*, *Mastocarpus stellatus*	Thallus size (+), Species (–)
8	Gaylord *et al.* (1994)	1,1,1	*Mazzaella leptorhyncos*, *M. flaccida*, *Pelvetiopsis limitata*	Thallus size (+), Species (–)
9	Johnson & Koehl (1994)	1,3,3	*Nereocystis luetkeana*	Wave exposure (–), Season (+)
10	Denny (1995)	1,1,1	*Mastocarpus papillatus*	Thallus size (–)
11	Friedland & Denny (1995)	1,1,1	*Egregia menziesii*	Thallus size (+)[b], Wave exposure (+)
12	Hawes & Smith (1995)	1,1,1	*Ulva lacutuca*	Thallus size (–), *In-situ* vs. Flume tests (–)
13	Molloy & Bolton (1996)	3,1,1	*Laminaria schinzii*	Wave exposure (–)
14	Shaughnessy *et al.* (1996)	1,2,1	*Mazzaella splendens*, *M. linearis*	Thallus size (+), Ploidy level (–), Species (–)
15	Utter & Denny (1996)	1,1,1	*Macrocystis pyrifera*	None
16	van Tamelen & Stekoll (1996)	1,2,1	*Fucus gardneri*	Wave exposure (–), Substratum (+)
17	Blanchette (1997)	1,2,3	*Fucus gardneri*	Thallus size (+), Wave exposure (?)[c], Season (+)
18	Collado-Vides *et al.* (1998)	1,2,1	*Udotea flabellum*	Habitat (–)
19	Smith & Bayliss-Smith (1998)	1,1,1	*Durvillaea antarctica*	None
20	Kawamata (2000)	1,2,5	*Laminaria japonica*	Life-stage (Thallus size) (+), Wave exposure (+)
21	Milligan & DeWreede (2000)	1,2,2	*Hedophyllum sessile*	exposure (+for juveniles, – for adults), Substratum (+ for juveniles), Season (– for adults), Direction of pull (– for adults)
22	Carrington *et al.* (2001)	1,2,1	*Chondrus crispus*	Ploidy level (–)
23	Duggins *et al.* (2001)	1,1,1	*Nereocystis luetkeana*	Wounding (+)
24	Kawamata (2001)	1,3,1	*Laminaria japonica*	Wave exposure (+), Substratum (–)
25	Blanchette *et al.* (2002)	2,1,1	*Egregia menziesii*	Wave exposure (+)
26	Haring *et al.* (2002)	1,1,2	*Fucus gardneri*	Desiccation (+)
27	Pratt & Johnson (2002)	1,2,4	*Chondrus crispus*, *Mastocarpus stellatus*	Wave exposure (–), Season (+), Species (–)
28	Wikström *et al.* (2002)	2,1,1	*Fucus evanescens*, *F. serratus* (*F. vesiculosus*)	Species (+), Locality (–)
29	Malm *et al.* (2003)	1,2,1	*Fucus vesiculosus*	Exposure (–), Substratum (+)
30	Duggins *et al.* (2003)	6,1,1	*Agarum fimbriatum*, *Costaria costata*	Size (+), Exposure (+)

[a] No formal statistics provided, the conclusion was based on a re-analysis of extracted data. [b] Only for exposed individuals. [c] Unknown as break forces for exposed & protected populations were pooled.

and stipe-strength studies, where the break force equals the stipe strength multiplied by the cross-sectional area of the stipe (Holbrook *et al.*, 1991; Utter & Denny, 1996; Smith & Bayliss-Smith, 1998; Duggins *et al.*, 2001), were included to add some of the larger kelps to the database, or if preliminary tests had demonstrated similarities between *in situ* tests and stipe-extension tests (Pratt & Johnson, 2002). Potential problems with using stipe-extension tests are that algae do not always break at the stipe during storms (Carrington, 1990; Shaughnessy *et al.*, 1996; Milligan & DeWreede, 2000) and that artefacts associated with bringing algae to the laboratory and using cut tissue-sections are unknown.

Simple vote counting was used to assess the relative importance of the investigated factors because in most cases data were too scarce, non-standardized and inadequate for quantitative meta-analysis (Englund *et al.*, 1999; Osenberg *et al.*, 1999). To test for the presence of an allometric relationship between thallus size and break force, each variable was Log_{10}-transformed and checked for homogeneity of variances (Cochran's C-test, $p > 0.05$). A product-moment correlation analysis was used to ensure a significant correlation before reduced major axis regression was carried out to quantify the slope and intercept (Legendre, 2001; Quinn & Keough, 2002).

Results

We found 30 studies reporting break forces from 118 populations of 27 species from 19 genera and 6 orders of macroalgae (Table 1; Appendices 1 and 2). An additional study measured break forces for *Ascophyllum nodosum* (McEachreon & Thomas, 1987) but, because break forces were only reported standardized to algal biomass, break forces *per se* could not be evaluated and the study was not included in our analysis. Algae within the orders Laminariales (48 populations, 10 species), Gigartinales (37 populations, 8 species), and Fucales (28 populations, 6 species) were most frequently studied. Most studies were from North America (21 studies), the remaining studies being from Australasia (2 studies), Africa (2 studies), Asia (2 studies) and Europe (3 studies). All studies except one tropical (Mexico) and two near-polar (Alaska, Macquarie Islands) were from temperate regions, and intertidal studies were twice as common as subtidal studies (20 vs. 10). The most common study objective was to test effects of wave exposure (14 studies, 7 with significant effects) followed by testing effects of intra-specific thallus size (10 studies, including life-stage tests, 6 with significant effects), species (6 studies, 1 with significant effect), substratum (5 studies, 3 with significant effects), seasons (4 studies, 3 with significant effects), ploidy level (2 studies with no significant effects), habitat types (1 study with no effect), wounding (1 study with significant effect), desiccation (1 study with significant effect), *in situ* vs. laboratory-flume break forces (1 study with no effect), direction of pull (1 study with no effect), locality (1 study with no effect) and aggregation (1 study with no effect). Three studies did not state any explicit test-objectives and appeared to be purely descriptive. Of the 30 studies, only two measured break forces from more than three localities and/or sites (we define localities as sampling areas spatially separated by more than approximately 10 km, and sites as areas separated by less than approximately 10 km). Similarly, only two studies measured break forces from the same location for a specific test-factor at more than three different time periods.

The population-based break forces (F_{break}) ranged from 0.7 to 1162 N (mean = 50.0, SD = 133.4, $n = 118$) and thallus sizes (A) from 0.0003 to 9.68 m^2 (mean = 0.2769, SD = 1.050, $n = 118$) (Fig. 1, Appendix 1). There was a significant positive correlation between Log_{10}-transformed thallus area and Log_{10}-transformed break force ($r = 0.67$; $p < 0.0001$) and this relationship was determined to be $\text{Log}_{10}\ (F_{\text{break}}) = 1.85 + 0.36 \times \text{Log}_{10}\ (A)$ ($\text{SE}_{\text{intercept}} = 0.08$; $\text{SE}_{\text{slope}} = 0.04$) across the 118 populations (Fig. 1).

Discussion

A range of ecological factors has been found to influence macroalgal break forces significantly, although, with a few exceptions, most have been inadequately studied. While there are strong taxonomic, habitat and geographic biases in the available studies, there is clear evidence that thallus size is an important factor scaling macroalgal break forces within and between species.

Break forces of macroalgae have been reasonably quantified only within the orders Laminariales, Fucales and Gigartinales. These orders are indeed relevant to focus on because they are conspicuous habitat formers in many marine habitats and they typically show adaptations to the hydrodynamic regime and survive well in wave-swept environments (Gerard, 1987; Friedland & Denny, 1995; Molloy & Bolton, 1996; Blanchette *et al.*, 2002). Further, in contrast to many algae from other orders with encrusting, turfing or small filamentous growth forms, these algae are physically easy to work with in that all have relatively well differentiated thalli amenable to *in situ* pull tests.

It is a common assumption from rocky wave-swept habitats that detachment implies mortality (Gaylord *et al.*, 1994; Denny, 1995; Friedland & Denny, 1995; Blanchette, 1997; Bell, 1999). While a reasonable assumption for many of the large

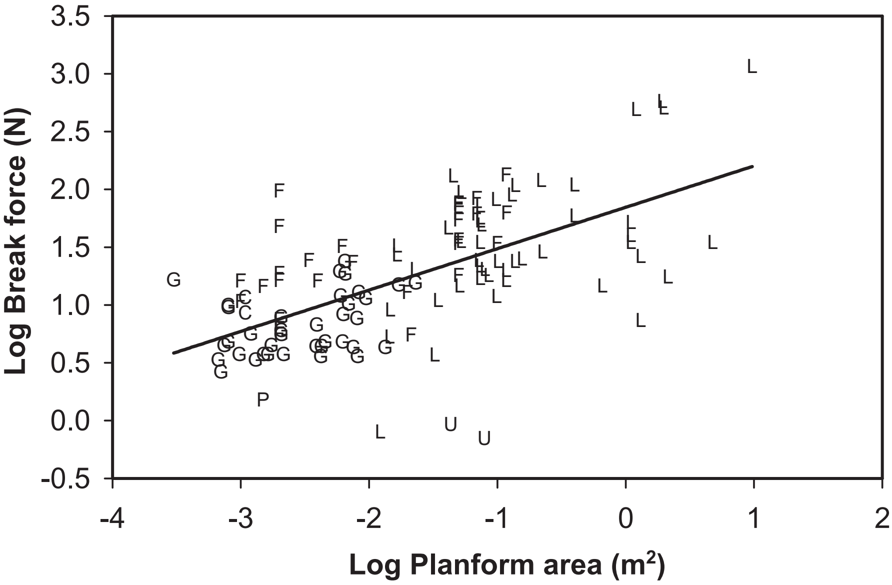

Fig. 1. Break force (F_{break}) *vs.* planform area (A) for 118 populations of macroalgae. $\mathrm{Log}_{10}(F_{break}) = 1.85 + 0.36 \times \mathrm{Log}_{10}(A)$ ($p < 0.0001$, $r^2 = 0.38$). The superimposed letters refer to the taxonomic order of each population. C = Caulerpales, F = Fucales, G = Gigartinales, L = Laminariales, P = Palmariales and U = Ulvales.

dominant macroalgae in these habitats, survival of algae in general is a complex function of several forms of hydrodynamic forces (Gaylord, 2000), the ability to reconfigure and streamline (Gaylord *et al.*, 1994; Denny, 1995), the exact break place (i.e., substratum, holdfast, stipe or frond; Carrington, 1990; Shaughnessy *et al.*, 1996), the ability to regenerate and recover from disturbances (Scrosati, 1998; Dudgeon *et al.*, 1999), the ability to re-attach (Santelices & Varela, 1994; Perrone & Cecere, 1997), the ability to survive in the drift (Cecere *et al.*, 1992; Lapointe, 1995) and the ability to reproduce or become reproductive in the drift (Bird & McLachlan, 1977; Norton, 1977). Hence, dislodgment or pruning is not ecologically adverse *per se* but can, in certain species, have a beneficial effect on survival, growth, reproduction and dispersal.

Several test factors including ploidy level (Shaughnessy *et al.*, 1996; Carrington *et al.*, 2001), direction of pull (Milligan & DeWreede, 2004), aggregation (Holbrook *et al.*, 1991), habitat type (Collado-Vides *et al.*, 1998), locality (Wikstrom *et al.*, 2002) and flume *vs.* pull breakage (Hawes & Smith, 1995) did not show significant effects on break forces. However, as these factors have been tested only in single studies (ploidy level excepted), it is premature to conclude that they generally are without importance to attachment mechanics, and further studies are recommended. In contrast, size (including life stage), substratum, wave exposure, season (temporal effects), species, desiccation and wounding were found to affect break forces significantly in at least one study, demonstrating the necessity to report the levels of these factors for each sampled population. Some studies reported non-significant relationships between break forces and thallus size (Carrington, 1990; Denny, 1995; Hawes & Smith, 1995). These studies, however, sampled only 'adult' macrothalli, and including a broader range of thallus sizes, such as small recruits, would likely produce significant effects of size (Shaughnessy *et al.*, 1996; Milligan & DeWreede, 2000). Interestingly, only half of the studies testing wave exposure found a significant effect on break force, suggesting that this factor may be less important than anticipated. Temporal variation, on the other hand, appears to be very important as three of four studies found a significant effect, probably because storms selectively remove weakly attached individuals and change (increase) the mean population break force overnight (Milligan & DeWreede, 2000; Pratt & Johnson, 2002). This highlights a logistic problem with comparing break forces of different populations in that *in situ* pull tests are time-consuming, making it difficult to sample several sites within a relatively short time-window. Thus, it is essential to ensure that the order of sites sampled has been randomized relative to any gradient or factor tested and that no storms have occurred between sampling events.

Most of the reviewed studies were mensurative experiments (*sensu* Hurlbert, 1984). In mensurative experiments, space and time are used to replicate the test-factors of interest and, if not carefully designed, these studies are susceptible to pseudoreplication and confounding (Hurlbert, 1984). Nested sampling in time and space is considered an efficient way to reduce these problems

(Underwood *et al.*, 2000), but only one out of the 30 studies reviewed applied such a design (Table 1, Jackelman & Bolton, 1990). For example, the studies testing effects of wave exposure generally compared populations from a few (usually two) different sites differing in wave exposure (e.g., Blanchette, 1997; Malm *et al.*, 2003; Milligan & DeWreede, 2000; Pratt & Johnson, 2002; van Tamelen & Stekoll, 1996) pseudo-replicating the exposure factor by sampling populations within each site (i.e., within the same unit of exposure) and thus potentially confounding the effects of wave exposure with other factors that often co-vary among sites such as substratum (Wells *et al.*, 1989), temperature (Blanchette *et al.*, 2002), nutrient concentration (Blanchette *et al.*, 2002), sedimentation (Airoldi & Cinelli, 1997; Airoldi, 1998) or grazing (Kawamata, 1998; Duggins *et al.*, 2001). Other comparisons were also potentially difficult to interpret. For example, all studies of seasonal effects included only one sampling event per season, providing no measure of variation within seasons to compare among seasons. Similarly, some comparisons of sites of different wave exposures were confounded by effects of different sampling times (Johnson & Koehl, 1994), and some ontogenetic effects were confounded by substratum in that juveniles were attached to other algae (a weak substratum) and adults were attached to rocks (a hard substratum) (Milligan & DeWreede, 2000).

Our population-based test found a highly significant positive relationship between break force and thallus size. This test included a wide range of species, exposure levels, substratum conditions, localities and sampling times, so that it provides strong support for the hypothesis that size is an overridingly important factor dictating break forces of macroalgae. Macroalgal strength (break force per cross-sectional area) is relatively constant among species (Denny *et al.*, 1989; Koehl, 2000) and the relationship between thallus size and break force was not unexpected since the cross-sectional area of a thallus varies in proportion to its area (allometric scaling). However, the relationship between break force and thallus size could not necessarily have been predicted from simple allometric scaling: some macroalgae do not scale their stipe diameter with thallus size (Carrington, 1990) and others fail at weak points in the substratum (Barnes and Topinka 1969), at grazing and abrasion scars (Duggins *et al.*, 2001) or because their thalli weaken due to ageing and tissue fatigue (Dudgeon & Johnson, 1992). These factors probably provide important contributions to the scatter of data observed in Fig. 1.

There are substantial differences among macroalgal taxa with respect to many important physiological and ecological properties, but so far there is only limited evidence to suggest that taxonomy *per se* affects break force (cf. Table 1). Taxonomy may however be important because it often co-varies with size. This is illustrated by the data provided in Appendices 1 and 2 (extracted data of corresponding thallus sizes and break force) where, disregarding the taxonomic biases in the available data (some species clearly either over- or under-represented), differences in break forces among populations of the taxonomic orders Gigartinales, Fucales and Laminariales (one-way ANOVA, Log_{10}-transformed data, $F_{(2,118)} = 41.2$; $p < 0.001$) are consistent with differences in thallus size (one-way ANOVA, Log_{10}-transformed data, $F_{(2,118)} = 90.9$, $p < 0.001$; *post hoc* SNK-tests ($p < 0.05$): Gigartinales [mean = 7.98 N, 0.0048 m^2, $n = 37$]; Fucales [38.81 N, 0.032 m^2, $n = 28$]; Laminariales [93.47 N, 0.6617 m^2, $n = 48$]). Different groups of algae have different gross morphologies, modes of attachment and investment in attachment structures relative to photosynthetic frond and reproductive structures. We therefore expect that comparisons across a wider range of groups will reveal differences among taxa, and we do not dismiss the notion that taxonomy may be important, but simply observe that size itself is a good starting point for understanding the attachment and break forces of macroalgae. Along the same lines we find it likely that systematic differences may emerge across non-taxonomic groups based on, for example, form, function, growth form or reproductive strategy.

Many studies did not report the mean thallus size of the populations sampled (van Tamelen & Stekoll, 1996; Carrington *et al.*, 2001; Duggins *et al.*, 2001; Blanchette *et al.*, 2002; Haring *et al.*, 2002; Wikstrom *et al.*, 2002; Malm *et al.*, 2003). While this was not an issue in the context of the individual studies, it makes comparisons among studies difficult. Similarly, because break force and thallus size typically co-vary (Fig. 1; Appendix 1) it is difficult to compare break forces between populations if one of the two variables is reported only for pooled populations (e.g., Blanchette, 1997; Collado-Vides *et al.*, 1998). The lack of information forced us to make several assumptions and generalizations about thallus sizes (cf. Appendices 1 and 2), obviously constraining the regression. Thus, to facilitate more sophisticated meta-analyses of break force data in future, we recommend that corresponding values of mean, standard deviation and level of replication for both break force and thallus size (e.g., wet weight) for each population and for all test factor combinations should always be reported. Scatter plots of thallus size vs. break force (e.g., Friedland & Denny, 1995; Hawes & Smith, 1995; Duggins *et al.*, 2001; Duggins *et al.*, 2003) are particularly useful because data-extraction programs provide a strong tool for data access and thus flexible and more powerful meta-analysis. Also, we strongly encourage more focus on sampling designs, which in most cases should be nested with independent sites replicating the factor under investigation (Jackelman & Bolton, 1990). If the factor of interest is pseudo-replicated, the results should be interpreted conservatively, constraining the conclusions by outlining potentially co-varying factors (Blanchette *et al.*, 2002) to allow the reader to evaluate cause–effect relationships. It is our hope that expansion of the presented database will allow more precise predictions of the survival of macroalgae, for example by implementing break force and thallus size data into typical 'survival-models' (Gaylord *et al.*, 1994; Denny, 1995; Friedland & Denny, 1995; Blanchette, 1997; Bell, 1999).

In summary, there is reasonable evidence to conclude that thallus size, wave exposure, substratum and time of sampling are important ecological factors that influence macroalgal break forces. However, many other factors are likely to be important and, while some have been addressed briefly, there is still a need for more studies. Hitherto, most experimental designs have been lacking broad spatial and temporal replication. In addition, there are strong taxonomic, habitat and geographic biases in the available information, and we suggest that future studies should address these issues so that a more complete understanding of macroalgal attachment mechanics can be obtained.

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Appendix 1. Mean break force (F_{break}), 95% confidence limits (95% CL), number of replicates (*n*), and thallus area for 118 populations of macroalgae (Pop. no.) used in the regression (n/r = data not reported). Study no. and Test Factor refer to Table 1 where references and specific test results can be found. Abbreviations for taxonomic orders: Cau: Caulerpales; Fuc: Fucales; Gig: Gigartinales; Lam: Laminariales; Pal: Palmariales; Ulv: Ulvales. Break forces and thallus sizes were extracted from figures, tables, and the texts in a review of 30 published studies (Table 1; Appendix 2)

Study no.	Pop. no.	Species	Order	Test Factor	F_{break} (N)	95% CL (N)	n	Thallus area (m^2)
1	1	*Fucus vesiculosus*	Fuc	Soft substrate (barnacle)	5.54	3.45	6	0.0213
1	2	*F. vesiculosus*	Fuc	Hard substrate (rock)	12.94	7.80	8	0.0200
2	3	*Halosaccion glandiforme*	Pal	None	1.51	0.21	20	0.0015
3	4	*Fucus vesiculosus*	Fuc	Wave-exposed	83.39	40.79	4	0.0693
3	5	*F. vesiculosus*	Fuc	Wave-protected	61.31	25.59	4	0.0693
3	6	*Ascophyllum nodosum*	Fuc	Wave-exposed	133.66	63.45	4	0.1177
3	7	*A. nodosum*	Fuc	Wave-protected	62.54	28.40	4	0.1190
4	8	*Mastocarpus papillatus*	Gig	Thallus size	4.78	n/r	90	0.0008
5	9	*Gigartina radula*	Gig	Wave-exposed	23.97	1.16	20	0.0065
5	10	*G. radula*	Gig	Wave-intermediate exposed	11.36	0.59	20	0.0094
5	11	*G. radula*	Gig	Wave-protected	7.68	0.39	20	0.0080
5	12	*G. radula*	Gig	Wave-exposed	19.53	0.72	20	0.0059
5	13	*G. radula*	Gig	Wave-intermediate exposed	10.27	0.66	20	0.0069
5	14	*G. radula*	Gig	Wave-protected	8.31	0.58	20	0.0063
6	15	*Postelsia palmaeformis*	Lam	Clumped	27.30	2.70	39	0.0165
6	16	*P. palmaeformis*	Lam	Isolated	32.50	4.06	29	0.0165
7	17	*Chondrus crispus*	Gig	Thallus size	7.96	1.69	28	0.0021
7	18	*Mastocarpus stellatus*	Gig	Thallus size	5.66	0.54	37	0.0012
8	19	*Mazzaella leptorhyncos*	Gig	Thallus size	6.73	n/r	100	0.0039
8	20	*Pelvetiopsis limitata*	Fuc	Thallus size	24.39	n/r	100	0.0034
8	21	*Mazzaella flaccida*	Gig	Thallus size	12.89	n/r	100	0.0083
9	22	*Nereocystis luetkeana*	Lam	Wave-protected and August	26.40	7.69	7	1.3100
9	23	*N. luetkeana*	Lam	Wave-protected and September	7.37	0.73	11	1.3100
9	24	*N. luetkeana*	Lam	Wave-exposed and July	14.70	1.45	17	0.6600
9	25	*N. luetkeana*	Lam	Current-swept and July	17.50	2.70	9	2.1300
10	26	*Mastocarpus papillatus*	Gig	Thallus size	2.64	n/r	240	0.0007
11	27	*Egregia menziesii*	Lam	Wave-exposed	131.32	16.35	39	0.0452
11	28	*E. menziesii*	Lam	Wave-protected	93.85	15.01	40	0.0527
12	29	*Ulva lactuca*	Ulv	Thallus size and pulled *in situ*	0.93	0.22	52	0.0433
12	30	*U. lactuca*	Ulv	Thallus size and flume breakage	0.70	0.15	33	0.0793
13	31	*Laminaria schinzii*	Lam	Wave-protected	510.12	255.73	n/r	1.9800
13	32	*L. schinzii*	Lam	Wave-intermediate exposed	490.50	132.67	n/r	1.2100
13	33	*L. schinzii*	Lam	Wave-exposed	578.79	63.45	n/r	1.9250
14	34	*Mazzaella splendens*	Gig	Small and gametophyte	9.50	2.55	12	0.0008
14	35	*M. splendens*	Gig	Small and sporophyte	10.00	2.74	12	0.0008
14	36	*M. splendens*	Gig	Large and gametophyte	15.60	1.57	12	0.0230
14	37	*M. splendens*	Gig	Large and sporophyte	15.00	2.16	12	0.0170
14	38	*M. linearis*	Gig	Small	16.50	2.94	12	0.0003
14	39	*M. linearis*	Gig	Large and gametophyte	18.50	1.96	12	0.0065
14	40	*M. linearis*	Gig	Large and sporophyte	12.00	0.59	12	0.0060
15	41	*Macrocystis pyrifera*	Lam	None	34.80	43.50	25	4.7600
16	42	*Fucus gardneri*	Fuc	Wave-exposed and hard substrate (rock)	18.84	4.92	30	0.0020
16	43	*F. gardneri*	Fuc	Wave-exposed and soft substrate (barnacle)	7.54	4.92	30	0.0020
16	44	*F. gardneri*	Fuc	Wave-exposed and soft substrate (barnacle)	5.65	1.23	30	0.0020
16	45	*F. gardneri*	Fuc	Wave-protected and hard substrate (rock)	16.33	3.69	30	0.0020
16	46	*F. gardneri*	Fuc	Wave-protected and soft substrate (barnacle)	6.28	1.23	30	0.0020
17	47	*F. gardneri*	Fuc	Wave-protected and spring	16.25	n/r	50	0.0040
17	48	*F. gardneri*	Fuc	Wave-protected and summer	23.45	n/r	50	0.0075
17	49	*F. gardneri*	Fuc	Wave-protected and winter	32.22	n/r	50	0.0062
17	50	*F. gardneri*	Fuc	Wave-exposed and spring	10.71	n/r	50	0.0010
17	51	*F. gardneri*	Fuc	Wave-exposed and summer	14.44	n/r	50	0.0015
17	52	*F. gardneri*	Fuc	Wave-exposed and winter	16.15	n/r	50	0.0010
18	53	*Udotea flabellum*	Cau	Lagoon	8.62	1.59	29	0.0011
18	54	*U. flabellum*	Cau	Rear-reef	11.67	3.61	29	0.0011
19	55	*Durvillaea antarctica*	Lam	None	1161.50	16 762.04	10	9.6800
20	56	*Laminaria japonica*	Lam	Life stage 1 and wave-protected	5.30	1.21	7	0.0144
20	57	*L. japonica*	Lam	Life stage 2 and wave-protected	11.02	3.48	10	0.0346
20	58	*L. japonica*	Lam	Life stage 3 and wave-protected	14.61	4.05	10	0.0508
20	59	*L. japonica*	Lam	Life stage 4 and wave-protected	16.98	10.65	3	0.0735

(*continued*)

Appendix 1. Continued.

Study no.	Pop. no.	Species	Order	Test Factor	F_{break} (N)	95% CL (N)	n	Thallus area (m^2)
20	60	*L. japonica*	Lam	Life stage 4 and 120 days at wave-exposed	72.05	18.47	5	0.0735
20	61	*L. japonica*	Lam	Life stage 4 and 90 days at wave-exposed	56.61	16.21	5	0.0735
20	62	*L. japonica*	Lam	Life stage 4 and 60 days at wave-exposed	53.12	11.31	5	0.0735
20	63	*L. japonica*	Lam	Life stage 4 and 28 days at wave-exposed	34.78	16.59	5	0.0735
20	64	*L. japonica*	Lam	Life Stage 4 and 0 day at wave-exposed	21.86	9.80	5	0.0735
21	65	*Hedophyllum sessile*	Lam	Wave-exposed and hard substrate (articulated coralline) for juveniles	9.10	2.16	23	0.0146
21	66	*H. sessile*	Lam	Wave-protected and hard substrate (articulated coralline) for juveniles	3.70	1.96	23	0.0325
21	67	*H. sessile*	Lam	Wave-protected and soft substrate (crustose coralline) for juveniles	0.80	0.78	23	0.0122
21	68	*H. sessile*	Lam	Wave-exposed and summer for adults	82.00	19.60	13	0.0975
21	69	*H. sessile*	Lam	Wave-protected and summer for adults	90.00	19.60	13	0.1300
21	70	*H. sessile*	Lam	Wave-exposed and winter for adults	108.00	19.60	13	0.1381
21	71	*H. sessile*	Lam	Wave-protected and winter for adults	120.00	19.60	13	0.2194
22	72	*Chondrus crispus*	Gig	Gametophyte	6.03	0.91	47	0.0021
22	73	*C. crispus*	Gig	Sporophyte	5.55	1.35	10	0.0021
23	74	*Nereocystis luetkeana*	Lam	Wounding – none	52.00	n/r		1.1000
23	75	*N. luetkeana*	Lam	Wounding – 0.5 mm cut	40.00	n/r		1.1000
23	76	*N. luetkeana*	Lam	Wounding – 1 mm cut	35.00	n/r		1.1000
24	77	*Laminaria japonica*	Lam	Protected PVC plate surface	16.40	0.39	8	0.1174
24	78	*L. japonica*	Lam	Wave-exposed on PVC plate pulled at surface	49.10	1.01	10	0.0753
24	79	*L. japonica*	Lam	Wave-protected on rock pulled *in situ*	19.90	0.46	10	0.1174
24	80	*L. japonica*	Lam	Wave-protected on PVC plate pulled in lab.	11.97	1.39	11	0.0986
24	81	*L. japonica*	Lam	Wave-exposed on PVC plate pulled in lab.	24.31	6.05	12	0.0719
25	82	*Egregia menziesii*	Lam	Wave-exposed	110.00	n/r	30	0.4000
25	83	*E. menziesii*	Lam	Wave-protected	59.00	n/r	30	0.4000
26	84	*Fucus gardneri*	Fuc	None	96.71	44.31	13	0.0020
26	85	*F. gardneri*	Fuc	None	47.73	7.39	43	0.0020
27	86	*Chondrus crispus*	Gig	Wave-protected and summer	4.31	0.61	20	0.0133
27	87	*C. crispus*	Gig	Wave-exposed and summer	4.31	0.61	20	0.0075
27	88	*C. crispus*	Gig	Wave-protected and autumn	3.59	0.41	20	0.0081
27	89	*C. crispus*	Gig	Wave-exposed and autumn	3.59	0.41	20	0.0042
27	90	*C. crispus*	Gig	Wave-protected and winter	4.82	0.90	20	0.0062
27	91	*C. crispus*	Gig	Wave-exposed and winter	4.82	0.90	20	0.0045
27	92	*C. crispus*	Gig	Wave-protected and spring	4.40	0.82	15	0.0042
27	93	*C. crispus*	Gig	Wave-exposed and spring	4.40	0.82	15	0.0039
27	94	*Mastocarpus stellatus*	Gig	Wave-protected and summer	3.75	0.69	15	0.0022
27	95	*M. stellatus*	Gig	Wave-exposed and summer	3.75	0.69	14	0.0015
27	96	*M. stellatus*	Gig	Wave-protected and autumn	3.75	0.65	20	0.0016
27	97	*M. stellatus*	Gig	Wave-exposed and autumn	3.75	0.65	20	0.0010
27	98	*M. stellatus*	Gig	Wave-protected and winter	4.50	0.63	20	0.0017
27	99	*M. stellatus*	Gig	Wave-exposed and winter	4.50	0.63	20	0.0007
27	100	*M. stellatus*	Gig	Wave-protected and spring	3.35	0.65	15	0.0007
27	101	*M. stellatus*	Gig	Wave-exposed and spring	3.35	0.65	14	0.0013
28	102	*Fucus serratus*	Fuc	None	34.20	42.53	24	0.1000
28	103	*F. evanescens*	Fuc	None	18.10	13.92	24	0.0500
29	104	*F. vesiculosus*	Fuc	Wave-exposed and soft substrate (amphibole)	34.30	6.86	33	0.0500
29	105	*F. vesiculosus*	Fuc	Wave-exposed and hard substrate (granite)	74.20	9.80	33	0.0500
29	106	*F. vesiculosus*	Fuc	Wave-exposed and hard substrate (sandstone)	76.40	31.75	33	0.0500
29	107	*F. vesiculosus*	Fuc	Wave-protected and soft substrate (amphibole)	36.60	8.82	47	0.0500
29	108	*F. vesiculosus*	Fuc	Wave-protected and hard substrate (granite)	62.60	8.23	47	0.0500
29	109	*F. vesiculosus*	Fuc	Wave-protected and hard substrate (sandstone)	54.40	13.33	47	0.0500
30	110	*Agarum fimbriatum*	Lam	Thallus size and wave-protected	23.70	3.92	n/r	0.1371
30	111	*A. fimbriatum*	Lam	Thallus size and wave-protected	18.00	3.72	n/r	0.0856
30	112	*A. fimbriatum*	Lam	Thallus size and wave-protected	35.50	7.84	n/r	0.0520
30	113	*A. fimbriatum*	Lam	Thallus size and wave-exposed	29.00	3.72	n/r	0.2255
30	114	*A. fimbriatum*	Lam	Thallus size and wave-exposed	25.20	3.53	n/r	0.1558
30	115	*Costaria costata*	Lam	Thallus size and wave-protected	20.30	4.12	n/r	0.0800
30	116	*C. costata*	Lam	Thallus size and wave-protected	23.90	2.94	n/r	0.1013
30	117	*C. costata*	Lam	Thallus size and wave-protected	20.40	4.51	n/r	0.0228
30	118	*C. costata*	Lam	Thallus size and wave-exposed	46.70	6.66	n/r	0.0414

Appendix 2. Details of extraction of break force and thallus area from 30 biomechanical studies (cf. Table 1). In studies reporting wet weight, a few simple planform area–biomass conversion factors were used where species-specific conversion factors were not available: Kelps = 11 cm^2 gWW^{-1}, and other algae (mainly fucoids) = 17.11 cm^2 gWW^{-1} (Thomsen & Wernberg, unpublished data). If no sizes were reported, size data corresponding to adult populations from other studies were used. Some studies measured break forces using a pull-test but only reported standardized stipe strength (Carrington, 1990; van Tamelen & Stekoll, 1996; Harrington *et al.*, 2002). Other studies measured stipe strength and reported standardized strength (Holbrook et al., 1991; Johnson & Koehl, 1994; Utter & Denny, 1996; Pratt & Johnson, 2002). Here, break forces were extracted by multiplication with stipe area. A few studies measured stipe strength but reported non-standardized break forces (Smith & Bayliss-Smith, 1998; Duggins *et al.*, 2001)

Study no.	Break force extraction	Thallus area extraction
1	Fig. 1	Fig. 1 (WW, ratio of 17 cm^2 gWW^{-1})
2	Text	Text (L = 8.2 cm, Vol. = 8.85 cm^3, formula for cylinder)
3	Fig. 2	Fig. 2 (WW, ratio of 17 cm^2 gWW^{-1})
4	Text (stipe strength), Fig. 8 (stipe diameter)	Fig. 8
5	Table 2	Table 2
6	Table 1 (stipe strength), Fig. 2 (stipe diameter)	Fig. 3 (WW, ratio of 11 cm^2 gWW^{-1})
7	Fig. 2	Fig. 2 (WW, ratio from Fig. 5)
8	Table 3	Text
9	Table 2 (stipe strength), Table 1 (stipe diameter)	Table 1 (A_{blade})
10	Table 9	Text
11	Fig. 7	Fig. 7
12	Text	Fig. 2
13	Text	Fig. 2 (WW, ratio of 11 cm^2 gWW^{-1})
14	Fig. 6	Fig. 4, small *M. linearis* from Fig. 1 (A = 33% of small *M. splendens*)
15	Fig. 6 (stipe strength), Text (stipe diameter)	Text (L = 18 m and reported Length–Area regression)
16	Fig. 3 (stipe strength, assumed break area of 12.4 mm^2 based on Blanchette, 1997)	Not reported (assumed A = 0.002 m^2, Blanchette, 1997)
17	Table 1 (data pooled from exposed and protected sites)	Fig. 4
18	Table 1	Fig. 4 (data pooled from back-reef and lagoon sites)
19	Table 2	Table 3
20	Figs 5, 6	Fig. 5 (WW, and ratio of 11 cm^2 gWW^{-1}, assumed A = 0.074 m^2 for populations portrayed in Fig. 6)
21	Figs 5, 8	Figs 5, 8, Table 3 (regression)
22	Fig. 2	Not reported (assumed A = 0.0021 m^2, Dudgeon & Johnson, 1992)
23	Fig. 9	Mean size not reported (assumed A = 1 kg WW and ratio of 11 cm^2 gWW^{-1})
24	Fig. 11, Table 5	Tables 4, 5
25	Fig. 9	Mean size not reported, (assumed A = 0.4 m^2 based on Fig. 7)
26	Fig. 6 (stipe strength, assumed break area of 12.4 mm^2 based on Blanchette, 1997)	Not reported (assumed A = 0.002 m^2, Blanchette, 1997)
27	Fig. 2	Fig. 1 (WW), 6 (regression)
28	Text (but not reported for *F. vesiculosus* which was in-between the two other fucoids)	Not reported (assumed A = 0.05 and 0.1 m^2 based on other fucalean studies)
29	Text	Not reported (assumed A = 0.05 m^2 based on other fucalean studies)
30	Table 3	Table 3 (regressions, and assuming site Y = site W)