



ELSEVIER

Aquatic Botany 80 (2004) 153–161

**Aquatic
botany**

www.elsevier.com/locate/aquabot

Short communication

Species, thallus size and substrate determine macroalgal break force and break location in a low-energy soft-bottom lagoon

Mads S. Thomsen*

Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA

Received 10 April 2004; received in revised form 10 August 2004; accepted 24 August 2004

Abstract

Biomechanical pull-tests were used to determine if thallus size and substrate type affect break force and break location of six macroalgal species (*Ulva curvata*, *Gracilaria verrucosa*, *Gracilaria foliifera*, *Agardhiella subulata*, *Fucus vesiculosus* and the alien *Codium fragile*) from a low-energy soft-bottom lagoon in Virginia, USA. Both small and large individuals of all six species incorporated into polychaeta (*Diopatra cuprea*) tube caps were weakly attached (<0.5 N), compared to individuals attached to bivalve shells (0.6–12.2 N). For algae attached to bivalve shells, *U. curvata* had the weakest attachment (small individuals = 0.6 N, large = 1.2 N), followed by *G. verrucosa* (2.5, 4.5 N), *A. subulata* (2.9, 4.4 N), *F. vesiculosus* (3.5, 8.4 N), *G. foliifera* (5.0, 7.6 N) and *C. fragile* (6.4, 12.2 N). Most species on shells had dislodgment (substrate-holdfast breakage) to pruning (algae breakage) ratios of ca. 50:50, compared to 90:10 on tube caps, suggesting that recovery following disturbances may be more important for individuals attached to shells. From break force and size data, mean break velocities were calculated for large individuals incorporated onto tube caps (the group most susceptible to hydrodynamic forces) to 0.4–1.2 m s⁻¹. Because currents often reach 1.5 m s⁻¹ in tidal lagoons, breakage may be common in these systems, limiting algal size, particularly when attached to soft substrates.

© 2004 Published by Elsevier B.V.

Keywords: Macroalgal break force; Dislodgment; Low energy lagoon; *Diopatra cuprea*

* Tel.: +1 434 924 0554; fax: +1 434 982 2137.

E-mail address: mads_thomsen@mailcity.com.

1. Introduction

In high-energy rocky habitats, waves can create extreme forces on sessile organisms, with water velocities exceeding 15 m s^{-1} , and exposure to such forces is considered a main cause of mortality (Denny, 1995). Biomechanical models have been applied to predict survival against hydrodynamic forces. In these models the break forces of sessile organisms are compared to the ambient hydrodynamic forces and the forces experienced by the organism. In this way break forces can be used to calculate break velocities, which are used to interpret susceptibility to waves and currents (Gaylord et al., 1994; Denny, 1995; Bell, 1999). Two of the most important factors determining macroalgal break forces are substrate type and thallus size (Gaylord et al., 1994; Milligan and DeWreede, 2000; Malm et al., 2003). Except for a few studies, most biomechanical algal research has been conducted in high-energy rocky systems (Thomsen, 2004). Here, I test if size and substrate type affect break forces of six algal species in a low-energy lagoon. To examine if breakage is a likely process affecting macroalgae in this lagoon, a second objective was to estimate break velocities and to compare these to typical lagoon velocities. Finally, because algae do not always dislodge (i.e. total biomass removal) under hydrodynamic stress, but may leave thallus fragments for regrowth (pruning, *sensu* Blanchette, 1997), a third objective was to test if species, thallus size or substrate type affected the break location. Together, these parameters give information about the likelihood of recovery after disturbances.

2. Methods

The study site, Hog Island Bay, Virginia, is a shallow soft-bottom lagoon situated on the Delmarva Peninsula (Thomsen, 2004). The macroalgae that are present year-round attached to bivalve shells were included in the study: *Ulva curvata*, the alien *Codium fragile* ssp. *tomentosoides*, *Fucus vesiculosus*, *Agardhiella subulata*, *Gracilaria verrucosa* and *G. foliifera* (Humm, 1979; Thomsen, 2004). *U. curvata* and *G. verrucosa* are also found incorporated into tube caps of the polychaeta *Diopatra cuprea* (Mangum et al., 1968; Thomsen and McGlathery, in press). Algae attached to shells and tube caps were sampled randomly in summer 2002 ($n \geq 30$ per species). To measure break force, a string was tied around the mid-thallus and pulled horizontal to the substrate with a spring scale (0.001 kg) until breakage. Shells and tube caps were fixed in space before a pull test, in order to simulate the immobile substrates of tube caps and consolidated oyster reefs in the lagoon. Wet weight (WW) was then determined for each individual after blotting with a towel. Break location was classified as either breaking at the substrate (dislodgment), or with the majority of holdfast remaining to the lower thallus (pruning, recovery possible). Data were discarded if the break location was near the string. To obtain estimates of break forces for *A. subulata*, *C. fragile*, *F. vesiculosus* and *G. foliifera* incorporated onto tube caps, fragments were added to cages inserted around polychaetas in situ. Tube caps were removed to force the polychaetas to build new ones (Brenchley, 1976; Thomsen and McGlathery, in press), and regenerated caps with attached algae were collected two days later for pull-testing ($n = 15$ for each of the four

species). The effect on break location was tested with χ^2 -tests on the six species, two substrate types (tube cap versus shell) and two size classes (small versus large), pooling non-tested factors. To obtain the two size classes, individuals were arranged according to wet weight for each species and substrate type, and the heaviest half was simply defined as 'large'. The effect on break force was tested with ANOVA on species, substrate and size class, followed by Student–Newman–Keuls post hoc tests to differentiate treatments of specific interest. Species-specific allometric relationships between thallus biomass and break force were quantified with Model II linear regression. Data were log-transformed to fulfill test assumptions. Break velocities were estimated for each individual from the drag equation (Denny, 1995):

$$U_{\text{break}} = \left[\frac{(2 \times F_{\text{break}})}{(C_{\text{drag}} \times A_{\text{plan}} \times \rho)} \right]^{0.5}$$

U_{break} is the water velocity (m s^{-1}) required to break a macroalgae with break force F_{break} (N) and planform area A_{plan} (m^2), ρ the density of seawater (1026 kg m^{-3}) and C_{drag} the drag coefficient (dimensionless). Although C_{drag} can vary with size, morphology, species and velocity (Denny, 1995; Koehl, 2000), a constant of 0.1 was assumed, partly to keep the models as simple as possible, and partly because 0.1 is a typical drag coefficient for algae exposed to steady flows of $0.1\text{--}1 \text{ m s}^{-1}$ (Johnson and Koehl, 1994; Hawes and Smith, 1995; Koehl, 2000; Kawamata, 2001). To convert wet weight to planform area, $A_{\text{plan}}:\text{WW}$ ratios of $3.9 (\pm 1.0, C. \text{fragile})$, $9.8 (\pm 1.8, F. \text{vesiculosus})$, $10.0 (\pm 1.6, A. \text{subulata})$, $14.0 (\pm 2.5, G. \text{foliifera})$, $23.2 (\pm 7.8, G. \text{verrucosa})$ and $199.8 (\pm 23.0, U. \text{curvata}) \text{ cm}^2 \text{ g}^{-1}$ were applied ($\pm \text{S.D.}$, $n = 22$). These ratios were obtained from area-analysis in Scion Image of photos of algal fragments spread out on a white background, and by measuring the corresponding wet weight of the fragments. Finally, mean break velocities and log-linear models of thallus area versus break velocities were calculated. Because U_{break} is derived from thallus size, i.e. size and U_{break} are not independent, no inferential statistical tests were performed (no P -values reported). However, standard errors and Pearson correlation coefficients were still calculated as estimates of the models accuracy.

3. Results

There were significant effects on break location of species ($\chi^2 = 29$, d.f. = 5, $P = 0.001$, $n = 419$) and substrate ($\chi^2 = 4.76$, d.f. = 1, $P = 0.031$, $n = 419$), but not size class ($\chi^2 = 0.48$, d.f. = 1, $P = 0.484$, $n = 419$). Fig. 1A shows that algae on tube caps experienced more dislodgment than algae on shells, that *U. curvata* experienced less dislodgment than other species, and that all species except *U. curvata* experienced more dislodgment on tube caps than on shells. The heaviest/largest individuals were found for species with low $A_{\text{plan}}:\text{WW}$ ratios attached to bivalve shells. Also, individuals were always larger on bivalve shells compared to on tube caps (Fig. 1B). Break force effects were significant for all single factors and the substrate \times size and species \times size interactions (Table 1). Break forces were small for both small and large individuals of all six species incorporated into tube caps ($<0.5 \text{ N}$). However, for algae attached to bivalve

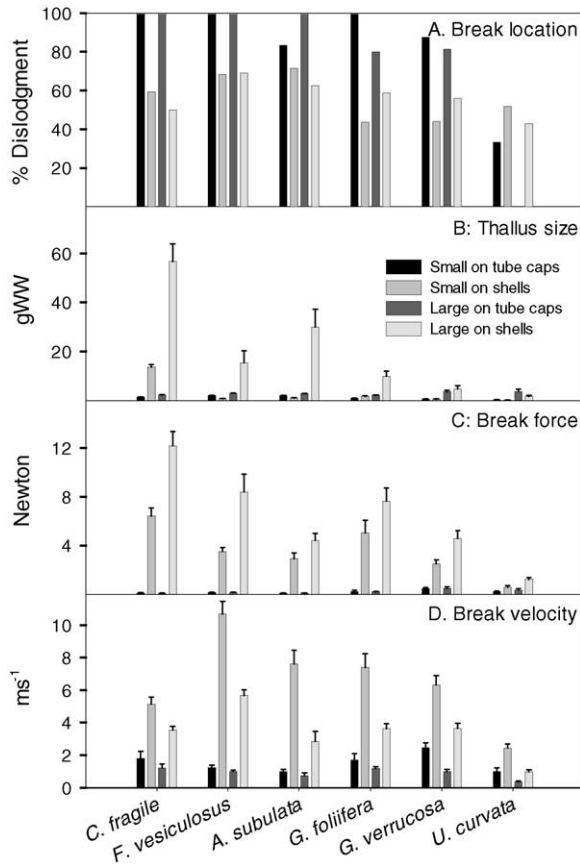


Fig. 1. Break location (A), thallus size (B), break force (C) and break velocity (D) for six algal species, two substrate types and two size classes (\pm S.E., cf. Table 1 for number of replicates). Species are arranged from low (left) to high surface area to wet weight ratios. Confer Table 1 for significant differences between groups for break force data.

shells, *U. curvata* clearly had the lowest break forces (small individuals = 0.6 N and large individuals = 1.2 N), followed by *G. verrucosa* (2.5, 4.5 N), *A. subulata* (2.9, 4.4 N), *F. vesiculosus* (3.5, 8.4 N), *G. foliifera* (5.0, 7.6 N) and *C. fragile* (6.4, 12.2 N) (Fig. 1C). Only *C. fragile*, *F. vesiculosus*, *G. verrucosa* and *G. foliifera* attached to bivalve shells had significant positive relationships between biomass and break force (Table 2, Fig. 2). Mean break velocities were calculated to be less than 1.3 m s⁻¹ for large individuals of all six species incorporated into tube caps (the group most susceptible to hydrodynamic forces) and ranging from 2.5 (*U. curvata*) to 10.6 (*F. vesiculosus*) m s⁻¹ for small individuals attached to bivalve shells (the group least susceptible to hydrodynamic forces) (Fig. 1D). Finally, all species on both substrate types had negative relationships between thallus size and break velocity, with highest correlation coefficients when attached to shells (Table 2).

Table 1
ANOVA on break force (log-transformed)

Source	d.f.	SS	F	P
Species (SPE)	5	27.28	14.40	0.000
Substrate (SUB)	1	128.67	859.67	0.000
Size (SIZ)	1	5.48	11.16	0.000
SPE*SUB	5	23.96	28.81	0.000
SPE*SIZ	5	0.29	0.55	0.876
SUB*SIZ	1	1.02	6.43	0.013
SPE*SUB*SIZ	5	0.48	0.58	0.716
Error	413	68.83		

Significant results ($P < 0.05$) are in bold. Confer Table 2 for number of replicates (divided into large vs. small sizes). Variance was heterogeneous for species (Cochran's C, $P = 0.01$). Break force differences (Student–Newman–Keuls post hoc tests): (a) *U. curvata* = *F. vesiculosus* = *G. foliifera* = *A. subulata* = *C. fragile* < *G. verrucosa* for algae incorporated to tube caps, (b) *U. curvata* < *F. vesiculosus* = *G. foliifera* = *A. subulata* = *G. verrucosa* < *C. fragile* for algae attached to shells, (c) tube caps incorporated algae < shell-attached algae for all species and (d) small < large individuals for all species.

Table 2
Linear models of log WW (g) vs. log F_{break} (N) and log A_{plan} (m²) vs. log U_{break} (m s⁻¹)

Species	Substrate	n	F_{break}				U_{break}		
			Slope	Intercept	r^2	P	Slope	Intercept	r^2
<i>C. fragile</i>	Tube cap	15	-0.27	-1.21	0.01	0.73	-0.63	-1.92	0.18
<i>F. vesiculosus</i>	Tube cap	15	-0.26	-0.77	0.02	0.60	-0.63	-1.63	0.34
<i>A. subulata</i>	Tube cap	15	-0.74	-0.87	0.06	0.39	-0.87	-2.39	0.25
<i>G. foliifera</i>	Tube cap	15	0.12	-0.79	0.01	0.80	-0.44	-1.08	0.20
<i>G. verrucosa</i>	Tube cap	32	0.18	-0.58	0.03	0.85	-0.41	-0.90	0.36
<i>U. curvata</i>	Tube cap	30	0.13	-0.77	0.03	0.86	-0.44	-1.13	0.58
<i>C. fragile</i>	Shell	64	0.37	0.35	0.17	0.00	-0.31	-0.06	0.38
<i>F. vesiculosus</i>	Shell	83	0.39	0.39	0.43	0.00	-0.30	-0.01	0.64
<i>A. subulata</i>	Shell	30	0.11	0.41	0.07	0.17	-0.45	-0.49	0.84
<i>G. foliifera</i>	Shell	33	0.35	0.52	0.38	0.00	-0.32	-0.09	0.67
<i>G. verrucosa</i>	Shell	50	0.35	0.41	0.29	0.00	-0.32	-0.19	0.58
<i>U. curvata</i>	Shell	55	0.16	0.21	0.03	0.19	-0.42	-0.83	0.49

Significant results ($P < 0.05$) are in bold.

4. Discussion

It is well-known that species, substrate type and thallus size affect biomechanical properties of macroalgae in high-energy wave-exposed rocky habitats (Gaylord et al., 1994; Denny, 1995; Blanchette, 1997; Milligan and DeWreede, 2000). Here, I document that these factors also determine biomechanical properties of macroalgae in low-energy soft-bottom systems.

The break location data showed no major differences between species and size groups for algae attached to shells. However, *U. curvata* differed from the five other species when incorporated onto *D. cuprea* tube caps by having a much higher likelihood of recovery

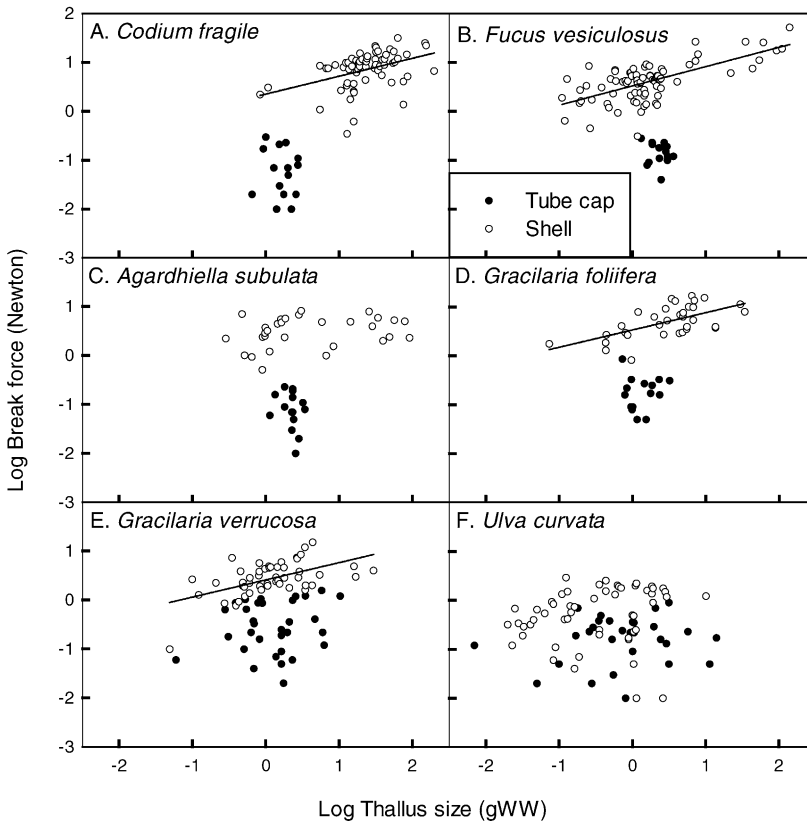


Fig. 2. Break force vs. thallus area for six algal species and two substrate types. Regression lines were added for significant relationships (cf. Table 2).

following a disturbance, suggesting that *D. cuprea* may facilitate *U. curvata* by providing an alternative and abundant substrate (Thomsen, 2004; Thomsen and McGlathery, in press). For the five other species incorporated onto tube caps, dislodgment was dominant and recovery would not be possible. This result may have implications for succession trajectories. If dislodgment occurs under hydrodynamic stress, new substrate becomes available and primary succession will follow. However, if pruning occurs, biogenic material will remain on the substrate and secondary succession will follow (Connell and Slatyer, 1977). In this case recolonization will depend on recovery abilities, in addition to propagule settlement and growth, and encroachment from neighbors. Field experiments should test if small-scale succession patterns differ between tube caps and shells with and without minute algal fragments.

Break forces were largest for algae attached to the hardest substrate, here shells, similar to findings from rocky systems (Milligan and DeWreede, 2000; Malm et al., 2003). Also, the species with the largest individuals and lowest surface area to wet weight ratio, had the highest break forces (Gaylord et al., 1994) although *A. subulata* had relatively low break

force for its size. For *U. curvata*, there were only small differences in break force between substrate types because its small/thin thallus, stipe and holdfast set a physical limit to its tissue strength. Thus, incorporation onto tube caps may be relatively more beneficial for small and opportunistic algae with weak attachment strengths (here *U. curvata*), partly because the substrate will be more unstable for large slow-growing species, and partly because opportunistic species have high regenerative abilities following pruning (Thomsen, 2004).

The break forces for large individuals attached to bivalve shells were relatively similar to break forces measured on algae from open rocky environments, e.g. *Fucus gardneri* (6–18 N, Blanchette, 1997), *Gigartina radula* (7–24 N, Jackelman and Bolton, 1990), *Mazzaella splendens* and *M. linearis* (9–19 N, Shaughnessy et al., 1996) and *Chondrus crispus* and *Mastocarpus stellatus* (3–6 N, Pratt and Johnson, 2002), suggesting that low-energy habitats do not facilitate uniquely low attachment forces. Four of the six species, *C. fragile*, *F. vesiculosus*, *G. verrucosa*, and *G. foliifera* had positive relationships between biomass and break force on bivalve shells, which occurs typically because large individuals have large attachment structures and thick stipes (Gaylord et al., 1994; Friedland and Denny, 1995). The relatively low r^2 values suggest that processes other than size and substrate affect break forces. Processes that contribute to break force variability at the population level include wounding and abrasion, age and senescence, nutritional/physiological status, genotypic variability, adaptations to local hydrodynamic conditions, and time of sampling with respect to hydrodynamic peak events (Johnson and Koehl, 1994; Blanchette, 1997; Milligan and DeWreede, 2000; Kawamata, 2001; Pratt and Johnson, 2002). It should be noted that the allometric relationships were insignificant for *U. curvata* and *A. subulata*, the two most opportunistic of the six species tested (Thomsen, 2004). This result is similar to findings for the opportunistic *U. lactuca* (Hawes and Smith, 1995) and *Egregia menziesii* from a wave-protected habitat (Denny, 1995). There were no relationships between thallus size and break force for any species incorporated onto tube caps, which is consistent with the finding that the strength of the binding is determined by the glue-sediment mix produced by the polychaeta (Mangum et al., 1968) instead of the tissue properties of the macroalgae.

All species on both substrate types had negative relationships between thallus size and break velocity, with highest correlation coefficients when attached to shells, supporting the hypothesis that larger marine algae may be limited by hydrodynamic forces (Gaylord et al., 1994; Denny, 1995). Thus, although most species had higher attachment force with larger thallus size, force did not scale with the estimated increase in drag (Hawes and Smith, 1995). The models provide a mechanistic explanation as to why taxa that grow into large individuals, such as *C. fragile*, *A. subulata* and *F. vesiculosus* rarely are found incorporated onto tube caps (Thomsen and McGlathery, in press). Alternative explanations include low encounter rates or low polychaeta preference (Thomsen, 2004). Tidal velocities within Hog Island Bay and other soft-bottom lagoons and estuaries are typically between 0.1 and 1.5 m s⁻¹ (Hawes and Smith, 1995; Albrecht, 1998; Lawson, 2003; Thomsen, 2004). Hence, breakage may be common for algae attached to soft substrates regardless of size, and for very large individuals attached to shells, particular for *U. curvata* and *A. subulata* which had the largest reduction in break velocities per size-increase. This is supported by tagging experiments that demonstrated typical mean 'survival' of less than a month for

algae on tube caps (Thomsen and McGlathery, in press) as well as low survival of *A. subulata* in wave-exposed localities (Thomsen, 2004).

It should be emphasized that the break velocity data only are first approximations. First, acceleration, impact and buoyancy forces were ignored in the models. However, the two first forces are likely of minor importance in tidal low-energy lagoons (Denny, 1995). In addition, Dromgoole (1982) showed that static lift was small compared to drag for the positively buoyant *C. fragile*. Second, it was assumed that algae attached to shells break or stay in place. This is a valid assumption if substrates are heavy and strong, such as healthy consolidated oyster reefs. However, algae are commonly attached to unconsolidated shells or partly eroded reef structures and entrainment of the algae-shell complex would be more likely than algal breakage (Dromgoole, 1982; Thomsen, 2004). Thus, size limitation caused by hydrodynamic forces is more likely to occur on heavy substrates, and explain why larger organisms are found on unconsolidated shells compared to consolidated-reef structures within Hog Island Bay (personal observations). Third, additional factors such as season, wave exposure level and wounding may influence break velocities (Blanchette, 1997) and wounding in particular will increase the risk of breakage. Finally, break velocities were calculated from a constant C_{drag} . As mentioned previously, C_{drag} varies with species, size, flow conditions, velocity and morphology (Denny, 1995; Koehl, 2000). Thus, the true break velocity can be underestimated or overestimated depending on whether the drag coefficient is higher or lower than what has been assumed here. In spite of the simplicity of the models, flume data generally supported the predicted break velocities for algae incorporated onto tube caps (Thomsen, 2004), and Hawes and Smith (1995) found a similar correspondence for *U. lactuca* on bivalve shells. Nevertheless, future biomechanical studies from low-energy soft-bottom habitats should include more test factors to expand on the current break force/velocity models, and more field (Bell, 1999) and flume (Hawes and Smith, 1995) experiments are clearly needed to test if form-, size-, species- and velocity-specific drag coefficients provide better break predictions (Bell, 1999; Koehl, 2000).

In conclusion, species and substrate determine algal break location, and species, substrate and size further determine break force and break velocity in a low-energy soft-bottom lagoon. Furthermore, dislodgment and pruning are likely to be common during peak hydrodynamic stress, but mainly for large individuals of opportunistic species, or if associated with soft substrates such as polychaeta worm tube caps.

Acknowledgments

Financial support was provided by the Danish Research Academy and Department of Environmental Sciences, University of Virginia. The manuscript benefited from comments from K. McGlathery, T. Wernberg and M. Vanderklift.

References

- Albrecht, A.S., 1998. Soft bottom versus hard rock: community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. *J. Exp. Mar. Biol. Ecol.* 229, 85–109.

- Bell, E.C., 1999. Applying flow tank measurements to the surf zone: predicting dislodgment of the *Gigartinaeae*. *Phycol. Res.* 47, 159–166.
- Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action—a case study with *Fucus gardneri*. *Ecology* 78, 1563–1578.
- Brenchley, G.A., 1976. Predator detection and avoidance: ornamentation of tube-caps of *Diopatra* spp. (Polychaeta: Onuphidae). *Mar. Biol.* 38, 179–188.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119–1144.
- Denny, M., 1995. Predicting physical disturbance—mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monog.* 65, 371–418.
- Dromgoole, F.I., 1982. The buoyant properties of *Codium*. *Botanica Marina* 25, 391–397.
- Friedland, M.T., Denny, M.W., 1995. Surviving hydrodynamic forces in a wave-swept environment—consequences of morphology in the Feather boa kelp, *Egregia menziesii* (Turner). *J. Exp. Mar. Biol. Ecol.* 190, 109–133.
- Gaylord, B., Blanchette, C.A., Denny, M.W., 1994. Mechanical consequences of size in wave swept algae. *Ecol. Monog.* 64, 287–313.
- Hawes, I., Smith, R., 1995. Effects of current velocity on the detachment of thalli of *Ulva lactuca* (Chlorophyta) in a New Zealand estuary. *J. Phycol.* 31, 875–880.
- Humm, H.J., 1979. The marine algae of Virginia. The University Press of Virginia, pp. 263.
- Jackelman, J.J., Bolton, J.J., 1990. Form variation and productivity of an intertidal foliose *Gigartina* species (Rhodophyta) in relation to wave exposure. *Hydrobiologia* 204/205, 57–64.
- Johnson, A.S., Koehl, M.A.R., 1994. Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats—thallus allometry and material properties of a giant kelp. *J. Exp. Biol.* 195, 381–410.
- Kawamata, S., 2001. Adaptive mechanical tolerance and dislodgment velocity of the kelp *Laminaria Japonica* in wave-induced water motion. *Mar. Ecol. Prog. Ser.* 211, 89–104.
- Koehl, M.A.R., 2000. Spatz, H.C., Speck, T. (Eds.), *Mechanical Design and Hydrodynamics of Blade-Like Algae: Chondracanthus exasperatus*, Thieme Verlag, Stuttgart, pp. 295–308.
- Lawson, S., 2003. Sediment suspension as a control of light availability in a coastal lagoon. MS Thesis. Department of Environmental Science, University of Virginia, pp. 115.
- Malm, T., Kautsky, L., Claesson, T., 2003. The density and survival of *Fucus vesiculosus* L. (Fucales, Phaeophyta) on different bedrock types on a Baltic Sea moraine coast. *Botanica Marina* 46, 256–262.
- Mangum, C.P., Santos, S.L., Rhodes, W.R., 1968. Distribution and feeding in the onuphid polychaeta, *Diopatra cuprea* (BOSC). *Mar. Biol.* 2, 33–40.
- Milligan, K.L.D., DeWreede, R.E., 2000. Variations in holdfast attachment mechanics with developmental stage, substratum-type, season, and wave-exposure for the intertidal kelp species *Hedophyllum sessile* (C. Agardh) Setchell. *J. Exp. Mar. Biol. Ecol.* 254, 189–209.
- Pratt, M.C., Johnson, A.S., 2002. Strength, drag, dislodgment of two competing intertidal algae from two wave exposures and four seasons. *J. Exp. Mar. Biol. Ecol.* 272, 71–101.
- Shaughnessy, F.J., De Wreede, R.E., Bell, E.C., 1996. Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Mar. Ecol. Prog. Ser.* 136, 257–266.
- Thomsen, M.S., 2004. Macroalgal distribution patterns and ecological performances in a tidal coastal lagoon, with emphasis on the non-indigenous *Codium fragile* ssp. *tomentosoides*. Ph.D. thesis. Department of Environmental Sciences, University of Virginia, Charlottesville, pp. 315
- Thomsen, M.S., McGlathery, K., in press. Facilitation of macroalgae by the sedimentary tube forming polychaeta *Diopatra cuprea*. *J. Estuarine, Coastal Shelf Sci.*