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Aquatic Botany 82 (2005) 168–180

Aquatic botany

www.elsevier.com/locate/aquabot

Holdfast aggregation in relation to morphology, age, attachment and drag for the kelp *Ecklonia radiata*

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Received 16 August 2004; received in revised form 4 February 2005; accepted 13 April 2005

Abstract

This study quantified the prevalence of holdfast aggregation (fusion of holdfasts) for the kelp *Ecklonia radiata* on subtidal reefs in southwestern Australia, and tested whether morphology, age, attachment or drag were different between kelps growing alone (solitary) or in aggregates. Wave-sheltered in-shore reefs consistently had fewer aggregates than wave-exposed off-shore reefs (15–20% versus 20–30%). On average, individual thalli from aggregates were longer (97.8 cm ± 2.2 S.E. versus 88.0 cm ± 2.0 S.E.) and had smaller holdfasts (32.9 g fresh wt ± 1.7 S.E. versus 45.8 g fresh wt ± 2.9 S.E.) than solitary thalli, whereas there were no significant differences in other morphological characters, including total biomass (805.1 g fresh wt ± 38.7 S.E. versus 831.5 g fresh wt ± 38.5 S.E.), stipe length (7.93 cm ± 0.47 S.E. versus 7.65 cm ± 0.40 S.E.) and stipe diameter (12.6 mm ± 0.23 S.E. versus 13.0 mm ± 0.25 S.E.). There was no difference in age between solitary (2.7–3.0 years) and aggregated (2.4–2.8 years) individuals. While the attachment force of whole aggregates (256.5 N ± 21.6 S.E.) was found to be significantly larger than attachment force for solitary individuals (162.5 N ± 12.9 S.E.), attachment areas were also larger for aggregates (90.7 cm^2 ± 5.40 S.E. versus 64.3 cm^2 ± 5.54 S.E.) and consequently there were no differences in attachment strength between aggregates (2.92 $\mathrm{N\,cm}^{-2}$ ± 0.26 S.E.) and solitary thalli (2.71 $\mathrm{N\,cm}^{-2}$ ± 0.22 S.E.). Aggregates had significantly smaller (17%) roughness factors (equivalent to drag coefficients) than solitary individuals and a negative relationship ($r = -0.68$) between roughness factors and biomass suggested that this was related to the scope for compaction and rearrangement of the thalli. Further, there was no relationship between roughness factors of solitary individuals and the aggregates they produced when combined, suggesting that roughness factors are

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doi:10.1016/j.aquabot.2005.04.003

not additive or multiplicative. The spatial distribution of holdfast aggregates, the morphological differences between solitary and aggregated individuals as well as their attachment and drag characteristics were all consistent with aggregation reducing the rate of fatal kelp dislodgment.

Keywords: Age; Aggregation; Attachment strength; Drag force; *Ecklonia radiata*; Kelp; Morphology; Wave exposure

1. Introduction

Macroalgae are commonly found in almost monospecific patches (Schiel, 1985; Holbrook et al., 1991; Piazzi et al., 2001) and within these patches the spatial distribution of thalli is often clumped (Rice, 1987; Goodsell et al., 2004). In some species, such as *Caulerpa* spp., clumping is caused by vegetative growth patterns (Piazzi et al., 2001) whereas in other species short dispersal distances of propagules may be responsible (Dayton, 1973).

The ecological significance of close proximity of macroalgae to conspecifics is not well understood. Macroalgae are known to affect their immediate physical environment (Eckman et al., 1989; Holbrook et al., 1991) and this can have both positive and negative effects on adjacent conspecifics. Positive effects may include protection from grazing (Velimirov and Griffiths, 1979; Anderson et al., 1997), ultraviolet light (Wood, 1987) or destructive hydrodynamic forces (Johnson, 2001), whereas negative effects may include shading (Kennelly, 1989; Holbrook et al., 1991), thallus abrasion (Velimirov and Griffiths, 1979) and mortality due to entanglement (Dayton et al., 1984).

Ecklonia radiata (C. Agardh) J. Agardh is a small perennial kelp that dominates subtidal reefs in temperate Australia (Wernberg et al., 2003b; Goodsell et al., 2004). *E. radiata* is a typical aclonal unitary macroalga (*sensu* Santelices, 2004) where the frond originates from a single stipe attached to a holdfast of haptera. Nevertheless, over years of sampling in *E. radiata* kelp beds, I have noticed that a large proportion of the adult sporophytes are found in aggregates where holdfasts of adjacent thalli are fused. Fused aggregates may arise either because spores settle in close proximity and develop concomitantly (Dayton, 1973; Critchley, 1983; Dayton et al., 1984) or because spores settle on or around the holdfasts of already established sporophytes (Anderson et al., 1997). Fusion of holdfasts and sporelings (coalescence) is well described for a range of red algae (Santelices et al., 1999) whereas there are only sporadic accounts of similar phenomena among brown algae (e.g., Critchley, 1983; Dayton et al., 1984; Paine, 1990; Anderson et al., 1997). Moreover, while some coalescent red algae result in chimeric forms where individuals become practically indistinguishable (Santelices et al., 1999 and references therein), the association between individuals within aggregates of *E. radiata* appears much more superficial with thalli apparently only sharing holdfast space (but see Paine, 1990 for observations suggesting a closer relationship). It is clear that the intimate association between coalescent red algae has important physiological, morphological and ecological consequences (Santelices et al., 1999; Santelices, 2004). In contrast, the implication of the loose associations between aggregated thalli of unitary algae, such as *E. radiata* is little known (see however, Holbrook et al., 1991).

Macroalgal morphology is known to vary with population density (Hymanson et al., 1990; Holbrook et al., 1991; Sjøtun and Fredriksen, 1995; Arenas and Fernandez, 2000). Because of the extreme proximity of thalli it seems reasonable to predict that aggregation will affect thallus morphology in a way consistent with density-dependent resource limitation, such as elongation (Hymanson et al., 1990; Holbrook et al., 1991; Sjøtun and Fredriksen, 1995) and reduced biomass (Arenas and Fernandez, 2000). The closeness of thalli may also affect dislodgment rates. The predicted morphological changes (Gerard, 1987), sheltering and support of leeward thalli (Holbrook et al., 1991; Johnson, 2001) or compaction (Koehl and Alberte, 1988; Armstrong, 1989; Milligan and DeWreede, 2004) may reduce hydrodynamic drag in aggregates. Dislodgment where attachment is overcome by hydrodynamic drag can be a major mortality factor of *E. radiata* (Thomsen et al., 2004) and similar small kelps (Milligan and DeWreede, 2000; Duggins et al., 2003). The net effect of aggregation on dislodgment rates will depend on how the attachment of overlapping holdfasts is related to changes in hydrodynamic drag. If aggregation affects dislodgment rates by influencing either hydrodynamic drag or attachment strength it will imply that *E. radiata* populations from different hydrodynamic environments have different proportions of aggregates. Furthermore, if aggregates have different dislodgment rates than solitary thalli, differences in ages of individuals would be expected.

Consequently, in this study I tested the hypotheses that the relative abundance of holdfast aggregates were different between wave-sheltered in-shore and wave-exposed off-shore reefs, and that the distribution patterns were consistent with differences in morphology, age, attachment and drag between solitary and aggregated kelps.

2. Materials and methods

2.1. Holdfast density and prevalence of aggregation

The density of kelp holdfasts was quantified during summer and autumn on limestone reefs at two southwest Australian locations approximately 400 km apart; Marmion Lagoon (31°49.5′S 115°42.0′E) and Hamelin Bay (34°13.5′S 115°00.5′E). Despite their names, both locations represent exposed open coast environments. The southwest Australian coastline is micro-tidal so the hydrodynamic environment is entirely dominated by seas and swell at both locations. At each location, three off-shore (wave-exposed) and three in-shore (wave-sheltered) 6–8 m deep sites were selected 1–5 km apart. At each site twenty 1 m^2 quadrats were haphazardly placed 1–5 m apart within *E. radiata* patches of 60–80% canopy cover. The number of holdfasts supporting mature kelp sporophytes (stage 3, Kirkman, 1981) was counted within each quadrat, and while counting it was noted whether the holdfasts were growing alone (solitary) or aggregated (fused) with adjacent holdfasts. Differences in holdfast densities and frequencies of aggregation (% of holdfasts) were tested with three-way ANOVA.

2.2. Morphology and age

Individual kelp thalli growing solitary ($n = 52$) or in aggregates ($n = 52$) were collected haphazardly from reefs throughout Marmion Lagoon and brought ashore for morphological measurements and age determination. Collections were made opportunistically over summer and autumn and always as equal numbers of solitary and aggregated thalli to avoid bias due to differences in sampling time or place. Morphological measurements included total length (stipe base to longest laminal apex), stipe length (stipe base to stipe apex), stipe diameter (immediately above holdfast), thallus fresh weight and holdfast fresh weight. Only one haphazardly selected thallus was measured from each aggregate. However, because it was often impossible to separate individual holdfasts within an aggregate, the compound holdfast was weighed and divided by the number of mature thalli in the aggregate. By far the majority of aggregates had only two thalli. The ages of kelp thalli were estimated by two different techniques as described for *E. radiata* from New Zealand (Novaczek, 1981): counting layers of haptera in the holdfast and cortical growth rings in the stipe. The age determinations were done as blind readings where haptera and stipes were labelled, mixed and processed without knowledge of their identity. Each morphological character and readings from both age determinations were then compared between solitary and aggregated thalli with Student's *t*-tests. Spearman rank correlation was used to assess the consistency of pairwise age readings.

2.3. Attachment strength

The attachment force of solitary thalli ($n = 19$) and whole aggregates ($n = 19$) was measured in situ in Marmion Lagoon during summer by pulling them off the reef with a 200 N or 350 N Pesola spring scale. A piece of nylon webbing was placed around the stipe(s) and attached to the spring scale. The pull was made at an angle of 30° to the substratum as one constant motion, slowly increasing force until the holdfast(s) came off. Samples where stipes broke before dislodgment were relatively few and were discarded. Holdfast attachment area was calculated as the area of an ellipsoid from measurements of the holdfast diameter in two perpendicular directions. Attachment force, area and strength (force standardised to holdfast area) were compared between solitary thalli and aggregates with a Student's *t*-test.

2.4. Drag force

Drag forces were measured on whole thalli cut immediately above their holdfasts. Holdfasts were not included because their largest surface, the attachment plane, does not obstruct flow when the kelps are attached to a reef. Kelp thalli were towed behind a boat at known speeds while force was measured with a Pesola spring scale. The kelps were connected to the spring scale via a non-flexible cord running on low-friction wheels along a vertical pole attached to the side of the boat. The pole, extending approximately 0.5 m into the water, and a 0.2 kg weight kept the kelp submerged, out of the wake of the boat. The background drag created by the setup was measured without kelp and subtracted measurements with kelp. Drag was measured for both solitary thalli ($n = 16$) and aggregates ($n = 8$) where aggregates were constructed by randomly pairing the solitary thalli so that no thallus was used in more than one aggregate.

The relationship between the drag in an object, its size and the viscosity and velocity of the fluid is commonly described by the drag-equation (e.g., Vogel, 1984). However, the drag-equation is based on size measured as surface area and this can be very difficult to obtain for complex three-dimensional macroalgae, such as kelps, and therefore, Schutten and Davy (2000) proposed a simplified relationship of $D = A'' \times B \times U^{1.5}$, where D is the hydrodynamic drag (drag force), A'' the 'roughness factor', B the thallus biomass and U is the water velocity. Schutten and Davy (2000) demonstrated that this 'modified drag-equation' was very precise in modelling the relationship between drag, thallus biomass and water velocity for a wide range of morphologically distinct macrophytes. A'' is the main variable of interest in that it is analogous to the classic drag coefficient (Schutten and Davy, 2000) which, adjusting for size and fluid characteristics, directly relates objects and their resistance to flow (Vogel, 1984). Consequently, for each drag–velocity profile D was regressed on $B \times U^{1.5}$ and A'' derived as the slope of the resulting linear regression models.

3. Results

3.1. Holdfast density and aggregation frequency

There were no significant differences in holdfast density among locations or reef lines (Table 1) and the surveyed kelp patches had 12.8 holdfasts $\mathrm{m}^{-2} \pm 0.72$ S.E. ($n = 12$ sites). Fifteen to twenty percent of all holdfast units in Marmion Lagoon were fused aggregates of more than one holdfast whereas the corresponding values in Hamelin Bay were 20–30% (Fig. 1). Off-shore reefs had 5–10% more kelp aggregates than in-shore reefs at both locations and both differences between locations and reef lines were statistically significant (Table 1). The absence of significant interactions between any of the analysed factors indicated that the patterns among locations and reef lines (wave exposures) were consistent. There were however significant differences in holdfast densities among some

Table 1
Results from three-way mixed model analysis of variance testing the effect of reef line (in-shore, off-shore; fixed factor), location (Marmion Lagoon, Hamelin Bay; fixed factor) and sites nested within reef line (1–3; random factor) on kelp holdfast density and aggregation frequency

Source of variation	DF	Holdfast density		Holdfast aggregation frequency	
		MS	*F*	MS	*F*
Location	1	3.4121	17.6	76.456	26.1^{**}
Reef line	1	0.0511	0.08	47.426	9.34^{*}
Reef line × location	1	1.0232	5.27	1.2202	0.42
Site (reef line)	4	0.6643	4.64^{**}	5.0754	1.11
Location × site (reef line)	4	0.1940	1.35	2.9271	0.64
Residual	228	0.1433		4.5742	
Transformation and Cochran's *C*		$\log x$, $P < 0.05$	$C = 0.17$,	$x^{0.5}$, $C = 0.11$, $P > 0.05$	

Variance of holdfast densities remained heteroschedastic even after transformation and significance was therefore judged conservatively at: $^{*}P < 0.01$ and $^{**}P < 0.001$. For holdfast aggregation frequency: $^{*}P < 0.05$ and $^{**}P < 0.01$.

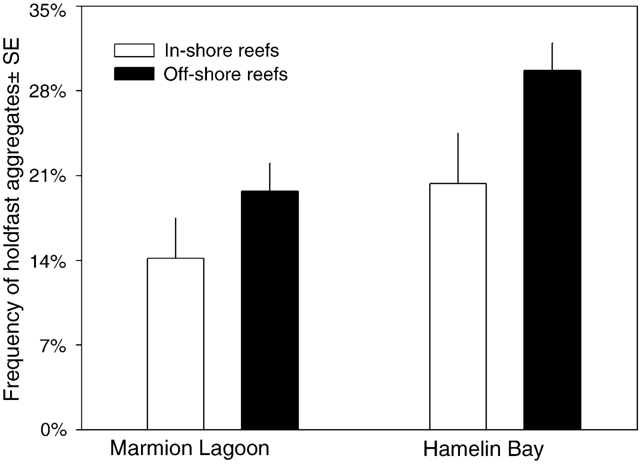

Fig. 1. Frequency of holdfast aggregates on in-shore (wave-sheltered) and off-shore (wave-exposed) reefs in Marmion Lagoon and Hamelin Bay; $n = 3$ sites where each site is the average of twenty 1 m^2 quadrats.

sites within reef lines and, at the quadrat-level there was a positive correlation between holdfast density and aggregation frequency ($r = 0.47$, $P < 0.001$, $n = 240$).

3.2. Morphology and age

Thallus length and holdfast biomass were highly significantly different between solitary and aggregated thalli (Table 2). Thallus biomass, stipe length and stipe diameter were not significantly different. Individual thalli from aggregates were about 10 cm longer (11%) and had about 15 g fresh weight lighter holdfasts (28%) than solitary individuals. There were no significant differences in age as measured by layers of haptera or numbers of cortical stipe rings and the mean age of both solitary and aggregated individuals was found to be just less than 3 years (Table 2). There was a poor agreement between ages determined by the two techniques (solitary individuals: Spearman's $r = 0.25$, $P = 0.07$; aggregated individuals: Spearman's $r = 0.10$, $P = 0.46$; $n = 52$ for both correlations).

Table 2
Morphological characters and ages of individual kelps growing alone (solitary) or in aggregates

	Solitary holdfast	Holdfast aggregate	*P*
Thallus length (cm)	88.0 ± 2.0	97.8 ± 2.2	0.001
Stipe length (cm)	7.65 ± 0.40	7.93 ± 0.47	0.63
Stipe diameter (mm)	13.0 ± 0.25	12.6 ± 0.23	0.20
Thallus biomass (g fresh wt)	831.5 ± 38.5	805.1 ± 38.7	0.63
Holdfast biomass (g fresh wt)	45.8 ± 2.9	32.9 ± 1.7	<0.001
Age – stipe rings (years)	3.0 ± 0.11	2.8 ± 0.11	0.18
Age – haptera (years)	2.7 ± 0.10	2.4 ± 0.11	0.07

Mean ± standard error, $n = 52$ for each group. *P*-value is level of significance in *t*-test between means.

Table 3
Holdfast attachment characteristics for kelps growing alone (solitary) and in aggregates

	Solitary holdfast	Holdfast aggregate	P
Attachment force (N)	162.5 ± 12.9	256.5 ± 21.6	<0.001
Holdfast attachment area (cm^2)	64.3 ± 5.4	90.7 ± 5.4	<0.001
Attachment strength ($\mathrm{N\,cm}^{-2}$)	2.71 ± 0.22	2.92 ± 0.26	0.53

Mean ± standard error, $n = 19$ for each group. P-value is level of significance in t-test for difference between means.

3.3. Attachment and drag

Aggregates of kelp were considerably more (58%) firmly attached to the limestone reef than solitary kelp thalli (Table 3). However, the attachment area was also larger (41%), and when adjusting for this inequality there were no differences in attachment strength between aggregates and solitary kelps (Table 3).

Drag force increased linearly with the product of water velocity$^{1.5}$ and biomass ($r^2 > 0.89$ in all cases, Fig. 2) across the range of experimental water velocities (~0.5–2.5 m s^{-1}). The roughness factor, A'' (i.e., slopes of regression models, Fig. 2), of kelp aggregates was lower (17%) than for solitary individuals (Fig. 3); this difference was statistically significant (paired t-test, mean of the two solitary individuals versus the aggregate, $t_{0.05(2),7} = 2.52$, $P = 0.04$, $n = 8$). There was no correlation between the roughness factor of solitary individuals and their aggregates ($r = 0.38$, $P = 0.36$, $n = 8$), but there was a strong negative correlation between A'' and biomass across both solitary kelps and aggregates ($r = -0.68$, $P < 0.001$, $n = 14$, Fig. 3).

4. Discussion

4.1. Prevalence of holdfast aggregation

Fusion of holdfasts between adjacent thalli is probably widespread in dense patches of macroalgae, which predominantly rely on reproduction by propagule dispersal (e.g., Critchley, 1983; Santelices et al., 1999). This study documented that fused aggregates of *E. radiata* holdfasts were common in Marmion Lagoon and Hamelin Bay, and that their frequency of occurrence varied consistently with the hydrodynamic environment. Not only was the proportion of holdfast aggregates consistently higher on exposed off-shore reefs than on sheltered in-shore reefs, it was also higher in Hamelin Bay than in Marmion Lagoon. These two locations reflect a large-scale gradient in exposure to ocean swell (Sanderson et al., 2000) because Marmion Lagoon is located where the continental shelf is wide with several submerged limestone ridges that provide some protection whereas Hamelin Bay is located where the shelf is narrow and steep, and only has a few small islands to attenuate swell energy.

There was a positive correlation between kelp density and aggregation frequency at the quadrat-level, likely reflecting that at high densities holdfasts occupy more space thus increasing the likelihood of contact and fusion. However, kelp densities were not different

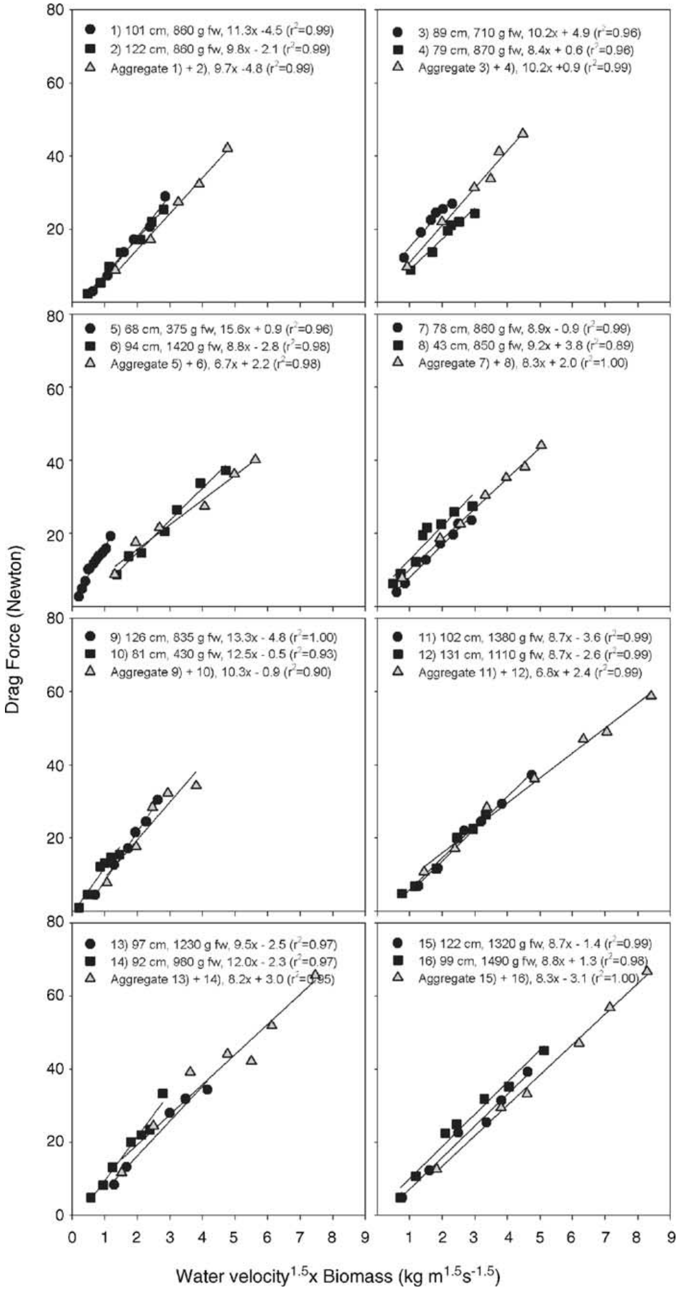

Fig. 2. Effect of water velocity$^{1.5}$ × biomass on drag force of solitary kelp thalli and aggregates constructed by combining two solitary thalli. Data given on the graphs are thallus length (from just above the holdfast to the end of the longest lateral), thallus fresh weight and linear regression models. The roughness factor, A'', is the slope of the models.

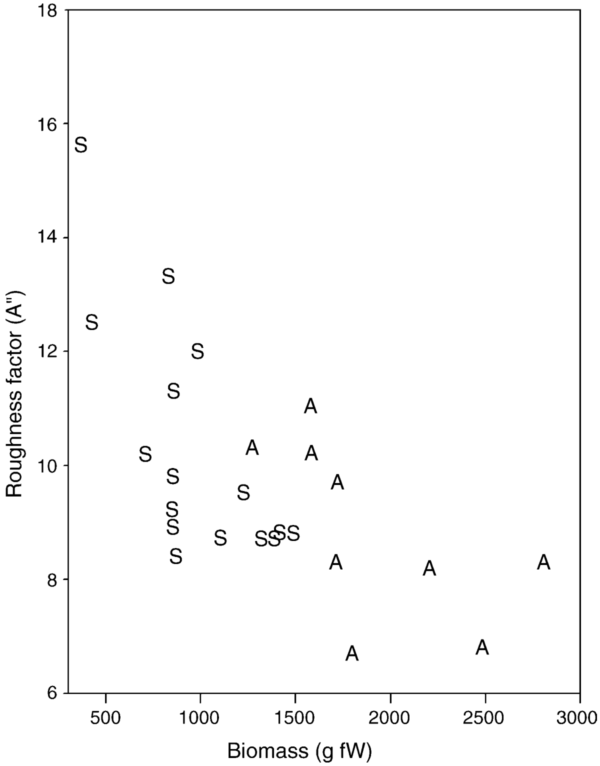

Fig. 3. Roughness factors of solitary (S) thalli and aggregates (A) of two thalli plotted against their biomass.

between reef lines or locations (this study) and kelp holdfast sizes (weights) are not different between sheltered and exposed reefs (Wernberg and Thomsen, in press). Consequently, neither kelp density or holdfast size confounded the patterns among locations or wave exposures.

The positive relationship between wave exposure and holdfast aggregation frequency suggests that aggregates either have a higher formation rate or a lower mortality rate than solitary individuals in exposed relative to more sheltered environments. Clumped distributions of macroalgae have previously been associated with reduced water motion in combination with limited dispersal (Dayton, 1973; Johnson and Brawley, 1998), and so, an increase in the formation rate of aggregates on exposed relative to sheltered reefs seems unlikely. In contrast, the morphological, attachment and drag characteristics associated with aggregated individuals are consistent with the alternative model that aggregates may have a lower mortality rate (see below).

4.2. Morphological differences

Morphological differences between solitary and aggregated thalli were apparent despite the fact that all individuals were collected from within relatively dense patches of kelp. Individuals in aggregates were 11% longer than solitary individuals. This difference may not appear substantial, however, it amounts to almost one quarter of the largest difference (48%) in total thallus length among *E. radiata* populations across 1000's of kilometers of Australasian coastline (Wernberg et al., 2003a). The larger thallus length but not biomass shows that aggregated kelps are more slender. This morphological difference is consistent with reduced drag (Gerard, 1987, but see Milligan and DeWreede, 2004). Elongation of thalli in aggregates is likely a response to increased shelf shading, as suggested for similar responses to crowding in other kelps, such as *Pterygophora californica* Ruprecht (Hymanson et al., 1990), *Postelsia palmaeformis* Ruprecht (Holbrook et al., 1991) and *Laminaria hyperborea* (Gunnerus) Foslie (Sjøtun and Fredriksen, 1995).

Per individual, holdfasts in aggregates were 28% smaller than solitary holdfasts. A positive relationship between wave exposure (and hence drag) and allocation of resources to holdfast structures has been found for *L. hyperborea* (Sjøtun and Fredriksen, 1995) and *Eisenia arborea* J.E. Areschoug (Roberson and Coyer, 2004). If a similar relationship exists for *E. radiata* – and there are indications it might – then, the observed differences in holdfast biomass are consistent with the idea that aggregation reduces perceived drag; although Wernberg and Thomsen (in press) found no differences in holdfast sizes across wave exposures, their data suggested that exposed thalli were smaller and thus that, relatively, holdfasts were larger in the high drag environment.

4.3. *Age*

Counting cortical growth rings has been successfully applied to determine the age of a range of perennial macroalgae (Hymanson et al., 1990 and references herein) including long-stiped *E. radiata* from New Zealand (Novaczek, 1981) and the Australian east coast (Larkum, 1986). In this study, both aging techniques provided similar estimates of 2–3 years mean ages for both solitary and aggregated individuals. This corresponds well with what would be expected from a reported mortality rate of >60% per annum for grown sporophytes in Marmion Lagoon (Hatcher et al., 1987). However, the poor correlation between individual ages determined by ring counts and haptera layers highlights limitations to the use of these methods. These limitations probably reflect that the confidence of the age-estimates is ±1 year for both methods (Novaczek, 1981; Hymanson et al., 1990), a large error when all individuals are 1–4-year-old. So, the methods may not be sensitive enough to detect subtle age differences among sub-populations, but they appear to still be useful to determine more coarse patterns in population structure.

4.4. *Attachment and drag*

Aggregates had higher attachment force than solitary individuals. Given the larger attachment area of the compound holdfast this was not surprising as several studies have found a positive relationship between attachment force and holdfast size or attachment area (Milligan and DeWreede, 2000; Kawamata, 2001; Duggins et al., 2003). After adjusting for attachment area there were no differences in attachment strength between aggregates and solitary individuals, perhaps reflecting that attachment strength is a constant determined by a combination of the species-specific attachment mechanism and substrate properties (e.g., degree of consolidation and rugosity). The lack of a difference in attachment strength between aggregates and solitary holdfasts is particularly interesting in light of the 28% smaller holdfasts per individual in aggregates because it suggests that they have obtained the same attachment strength with considerably less investment in holdfast structures. Holdfasts are relatively unproductive and hence, energetically, aggregation is advantageous, as there appear to be no negative consequences for thallus biomass.

Drag force is proportional to projected area (e.g., Vogel, 1984) and consequently biomass in many bladed aquatic macrophytes (Dudgeon and Johnson, 1992; Schutten and Davy, 2000). Davy and Schutten's (2000) equation provided an accurate relationship between water velocity, biomass and drag force, as indicated by the high r^2-values for the linear regression models. The roughness factors determined from these regression models all showed how the relative drag in aggregates is smaller than that of solitary individuals. When faced with increasing flow, the three-dimensional and digitate thallus-shape of algae, such as *E. raditata* will compact and rearrange (Koehl and Alberte, 1988; Armstrong, 1989; Milligan and DeWreede, 2004) to increase streamlining. The negative relationship between biomass and the roughness factor probably indicates that the relative amount of compaction and rearranging that can take place is limited by the three-dimensional size of the shape, i.e., the relatively larger volume (including interstitial space) of large specimens and aggregates have greater scope for compaction. There appear to be no straightforward relationships between the roughness factor of solitary individuals and the aggregates they produce when combined, suggesting that roughness factors are not additive or multiplicative.

Dislodgment, which is fatal to kelps, such as *E. radiata*, depends on a balance between attachment and drag. Per individual, aggregates had lower drag but similar attachment strengths compared to solitary kelps, suggesting that aggregation cause a relative reinforcement of the kelps. The distribution of holdfast aggregates relative to the hydrodynamic environment as well as morphological, attachment and drag differences between solitary and aggregated thalli were consistent with the notion that aggregation lowers the dislodgment rate. However, given the correlative nature of some of the evidence presented here, future studies should address these patterns by directly measuring dislodgment rates in tagging experiments and testing the causality of morphological differences in transplant experiments where kelp recruits are transplanted and grown alone (solitary) or in aggregates.

Acknowledgements

Grants from the Danish Natural Science Research Council and the Danish Research Academy supported this study. Data on attachment strength and drag were collected in collaboration with M.S. Thomsen. The Department for Conservation and Land Management, marine conservation branch, Perth, issued the permits to work within Marmion Marine Park. G.A. Kendrick and M.A. Vanderklift provided comments on early versions of the manuscript.

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