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

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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 N cm^{-2} ± 0.26 S.E.) and solitary thalli (2.71 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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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).