Disturbance initiates diversity in recruitment of canopy-forming algae: interactive effects of canopy-thinning and substratum availability

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We assessed whether disturbance within monospecific canopies (*Ecklonia radiata*, Phaeophyta) increases diversity of macroalgal recruits by creating gaps in the canopy and by liberating space on the substratum. We tested the hypothesis that a greater number of species of canopy-forming algae recruit to areas where canopies of monospecific *E. radiata* are thinned and the availability of barer substratum is increased (i.e. fewer holdfasts without thallus remain attached to the substratum). A significant interaction between canopy-cover and substrate-availability was detected; losses to canopy caused greater diversity of recruits only where there were few holdfasts were sparse, which were also found under dense canopies where remnant holdfasts were sparse, which were also found under dense canopies where remnant holdfasts may increase the likelihood of survival of recruits under dense canopies through the provision of habitat rather than displacing appropriate habitat for recruitment. Nevertheless, these results indicate that disturbance events not only initiate diversity of canopy-forming algae by thinning monospecific canopies, but through the liberation of available substratum.

INTRODUCTION

Disturbance is a key initiator of variability in the composition of taxa in many forest habitats (Pickett & White 1985; Kolasa & Pickett 1991). Competition between neighbouring individuals often results in the dominance of a few or single species (Paine & Levin 1981) which restricts the establishment of alternate species (Sousa 1979a, b). Disturbance is hence a principal process that can create and often maintains diversity of biogenic habitat through the loss of all, or parts of established individuals (Sousa 1984; Petraitis *et al.* 1989).

The severity of disturbance events and therefore the type of damage caused can vary greatly; not all disturbed patches are the same. Knowledge of the extent to which variation in the attributes of disturbed patches affect re-invasion is key to our understanding of the consequences of disturbance (Whittaker & Levin 1977; Peterson & Pickett 2000). In marine systems, tests of hypotheses about how the characteristics of disturbed patches affect the subsequent dynamics of recovery tend to focus on their size, shape or location (Connell & Keough 1985; Wernberg-Møller 2002; Airoldi 2003). When disturbances occur in biogenic habitat (e.g. forests of kelp) it is relatively unlikely that all organisms are completely removed (Foster & Sousa 1985). Despite such an obvious characteristic, there is little assessment of whether re-invasion is influenced by fragments of organisms remaining in disturbed patches (but see Kennelly 1987b; Underwood 1998).

Forests of brown algae are the major habitat for many marine animals of the temperate world (Witman & Dayton 2001). Three main types of assemblages of canopy-forming algae have been observed along rocky subtidal coastlines of Australia; monospecific *Ecklonia radiata* (C. Agardh) J. Agardh (Laminariales: Alariaceae) (Underwood *et al.* 1991; Kendrick *et al.* 1999), diverse assemblages of fucalean algae (Fucales) (Shepherd & Womersley 1970; Collings & Cheshire 1998) and complexes of fucalean species mixed with *E. radiata* (Goodsell *et al.* 2004). This small-scale variation in composition of forests of algae across temperate Australia may be driven by common disturbances such as storms and herbivory (Kennelly 1987a; Andrew & Jones 1990).

Depending on the particulars of the disturbance, removal of established canopy-forming algae often creates opportunities for the recruitment of alternate species thereby increasing the diversity of the canopy (Reed & Foster 1984). Dense Laminarian canopies can inhibit recruitment by modifying parameters of the physical environment such as light intensity (Schiel 1985; Kennelly 1989), water motion (Eckman et al. 1989) and by physically interfering with juveniles (Velimirov & Griffiths 1979; Connell 2003). Opportunities for recruitment and establishment of canopy-forming algae are therefore created when all or part of the surrounding adult plants are removed. Algal settlement is, however, dependant on space liberated in the canopy and on the availability and structure of the substratum (Dayton et al. 1984; Fletcher & Callow 1992). The two most extensive types of substrata in disturbed forests of algae which are available to recruits are holdfasts of canopy species or bare rock (Anderson et al. 1997).

Canopies of *E. radiata* are commonly thinned rather than completely removed (Kennelly 1987b). Moreover plants can be wholly dislodged or only partially removed leaving parts of the plant (usually the holdfast and stipe) remaining on the substratum (Andrew & Jones 1990). This means that although space is liberated in the canopy the substratum is still occupied by residual holdfasts. We tested the hypothesis that a

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Fig. 1. Location of study site; Spit Reef, West Island, South Australia.

greater number of species of canopy-forming algae recruit to areas where canopies of monospecific *E. radiata* are thinned and the availability of barer substratum is increased (i.e. fewer holdfasts without thallus remain attached to the substratum).

MATERIAL AND METHODS

Study site

This study was done on a subtidal reef (Spit Reef) off West Island, South Australia ($35^{\circ}37'S$, $138^{\circ}35'E$) (Fig. 1). The reef consists of granitic boulders 3-5 m deep and subject to primarily south-westerly swell. Stands of monospecific *E. radia-ta* were predominant, forming canopy approximately 60 cm high at the time of the study. Stands of mixed fucalean algae were also observed interspersed with areas of monospecific *E. radiata*. Detailed descriptions of the structure of assemblages of algae and environmental conditions at West Island are given by Shepherd & Womersley (1970). We counted and assessed the damage of *E. radiata* washed onto the shore at

West Island (n = 50) after a winter storm (Austral winter of 2002). A disproportionately large number of individuals did not have holdfasts, i.e. individuals were thallus and stipe only (n = 40) providing a biological basis for manipulations of the interactive effects of canopy thinning and availability of substratum.

Manipulating canopy-cover and substratum-availability

In Australia, cleared and disturbed patches created by storms in forests of E. radiata are seldom greater than a few square metres (Kennelly 1987a). We manipulated areas (1 m²) within forests of monospecific E. radiata to simulate common disturbance events (e.g. herbivory and storms). We removed whole plants (thallus and holdfast) from areas with very dense covers (> 14 individuals m⁻²) to manipulate canopy-cover to two levels: hereafter referred to as dense (7 individuals m⁻²) and sparse (3 individuals m⁻²). Individuals with holdfasts of similar size were selected from each plot and removed by levering the holdfast and plant carefully off the substratum with a dive knife. This procedure ensured the amount of free substratum created by removing plants was similar among plots within the two categories of canopy cover. Orthogonal to levels of canopy-cover, the availability of substratum was manipulated to create densely (7 holdfasts m⁻²) and sparsely distributed (3 holdfasts m⁻²) holdfasts without thallus attached by cutting the thallus from the base of the stipe. Criteria for the levels of density were chosen because a distinction between 'dense' and 'sparse' canopies of E. radiata at the above-mentioned levels influences the growth of understorey algae; increases in density above 7 plants m⁻² had no further effect on growth (Melville & Connell 2001).

Juvenile macroalgae visible to the naked eye were infrequent but if present were removed from all plots during manipulations. Six replicates of each treatment were randomly allocated on the reef. Manipulations were done in November of 2002. Plots were maintained over 4 months of the Austral spring and summer during which time the most abundant taxa of canopy-forming brown algae recruit at West Island (Alariaceae, Cystophoraceae and Sargassaceae) (Emmerson & Collings 1998; Hotchkiss 1999). Such a length of study is often used to determine factors important to the initiation of patterns of re-invasion (Kennelly 1983; Benedetti-Cecchi & Cinelli 1993; Melville & Connell 2001) and is sufficient for recruits to be identified as canopy-formers (approximately 5-10 cm high) (Kennelly 1987b; Kendrick & Walker 1994; Emmerson & Collings 1998). We acknowledge that other factors such as density-dependant competition (Schiel 1985; Reed 1990) and grazing (Kennelly 1983) are more influential in structuring and maintaining the composition of assemblages over longer periods of time.

Artefacts associated with cutting stipes to remove thalli, such as the release of phlorotannin or other chemicals, may confound results by inhibiting or cueing the recruitment of algae. To test for such artefacts, we cut seven sections (5–6 cm) of stipe from *E. radiata* individuals adjacent to our experiment site and attached one section to the stipe of each of seven existing, intact plants within very dense plots (14 individuals m⁻²) using cable ties (n = 6). These plots were maintained for the same duration as the experiment: 4 months. No significant difference was detected in the recruitment of



Fig. 2. Number of species of recruits of canopy-forming algae m⁻² (mean \pm SE) where residual holdfasts were dense (hatched bars) and sparse (open bars) under dense and sparse canopies (n = 6 replicates per treatment).

algae between these plots and very dense plots without cut stipes (ANOVA: $F_{1, 10} = 0.572$, P > 0.05). To control for the effects of removing whole plants we thinned very dense stands to a density of 7 plants m⁻² and maintained these for 4 months (n = 6). No significant difference was detected in the recruitment of algae between plots with natural density of 7 plants m⁻² and thinned plots (ANOVA: $F_{1, 10} = 3.244$, P > 0.05).

Sampling macroalgal recruits

Sampling in each plot was done by counting the species (> 5 cm in height) that form canopy as adults (similar to Kennelly 1987b; Emmerson & Collings 1998; Hotchkiss 1999). This also ensured that recruits were well established and should persist through permanent attachment to the substratum underneath holdfasts (Fletcher & Callow 1992) even after the

residual holdfasts have decayed (after > 6 months) (Anderson *et al.* 1997). No recruits were counted within 10 cm from the edge of the plot to avoid the effects of edges (Emmerson & Collings 1998). In each plot the amount of substrate free from holdfasts is inversely proportional to the total amount of residual and living holdfasts. For additional information, counts were partitioned into two categories: recruits attached to the substratum and recruits attached to residual holdfasts (without stipes) (only two individuals were observed on holdfasts with thalli attached). Counts were initially pooled to assess total recruitment in response to the treatments (canopy cover vs substrate availability) in analysis of variance (ANOVA). Type specimens were preserved and identified using keys from Womersley (1987) and are stored at The University of Adelaide, South Australia.

Analytical methods

Differences in the number of species (species richness) that recruited to disturbed plots were analysed using ANOVA. Where significant differences were detected, Student–Newman–Keuls tests were used *post hoc* to define among which groups differences existed. Data were tested for normality and heterogeneity beforehand to comply with the assumptions of ANOVA. Statistically significant results between groups were often difficult to detect using ANOVA because there was large variation between replicates. Nevertheless, biological patterns in the data seemed evident and Fisher's exact tests were used to determine the likelihood that observed outcomes appeared an equal number of times in both treatments by chance alone.

RESULTS

Seven species of algae were observed as recruits. Cystoseiraceae: *Cystophora moniliformis* (Esper) Womersley & Nizamuddin *ex* Womersley, *C. monilifera* (J. Agardh), *C. grevillei* (Agardh *ex* Sonder) J. Agardh and *Acrocarpia paniculata* (Turner) Areschoug, Sargassaceae: *Sargassum fallax* (Sonder), Seirococcaceae: *Syctothalia dorycarpa* (Turner) Greville and Alariaceae: *E. radiata*.

Losses to the canopy only caused changes in the richness of recruits where residual holdfasts were sparsely distributed but not where they were dense (Fig. 2; Table 1). ANOVA detected a significant interaction between the effects of can-

Table 1. (a) ANOVA of the mean number of species of recruits (species richness) between different covers of canopy (dense vs sparse) and densities of residual holdfasts (dense vs sparse) (inverse of substratum availability). Data were normally distributed (P < 0.05; Shapiro-Wilk test) and variance was homogenous (P > 0.05; Cochran's *C*-test). 'Canopy Cover' and 'Substrate Availability' were treated as fixed and orthogonal. (b) SNK tests for the significant interaction between canopy cover and substratum availability.

(a) ANOVA					
Source of variation		df	MS^1	F	P
Canopy cover		1	0.167	0.360	0.557
Substratum availability		1	0.167	0.360	0.557
Canopy cover \times substratum availability		1	4.167	8.930	0.007
Residual		20	0.467		
(b) SNK tests					
Dense canopy	Dense $>$ sparse holdfasts				
Sparse canopy	Dense = sparse holdfasts				
Dense holdfasts	Dense = sparse canopy				
Sparse holdfasts	Dense $<$ sparse canopy				

¹ MS, mean square.



Fig. 3. Mean abundance (\pm SE) of individual species m⁻² which showed substantial response to the availability of barer substratum; dense holdfasts (hatched bars) vs sparse holdfasts (open bars) under different covers of canopy (dense vs sparse) (n = 6 replicates per treatment).

opy cover and the availability of barer substratum on the species richness of recruits (Table 1). Where the cover of canopy was dense, richness in the assemblage of macroalgal recruits was greater where a larger number of residual holdfasts were present than smaller numbers (Fig. 2; Table 1).

No one individual species seemed responsible for differences in recruit assemblages among treatments. ANOVA for each taxon did not detect significant differences in the number of individuals of those taxa (attached to relatively bare substratum pooled with residual holdfasts) among treatments, except *C. monilifera* (greater under sparse than dense canopy, ANOVA: $F_{1, 20} = 10.29$, P < 0.05). Large variation between replicates (similar to Schiel 1985; Reed 1990; Santelices 1990) may have hampered the ability of ANOVA to detect statistically significant differences in patterns of recruit abundance between plots with different densities of canopy and substratum availability. The raw data indicates that total abundance of *C. grevillei* and *E. radiata* under dense canopies was larger where residual holdfasts were dense rather than sparse (Fig. 3). Under sparse canopies this pattern was also observed for *E. radiata*, but reversed for *C. grevillei* and did not exist for *S. fallax* (Fig. 3).

Three species were frequently observed attached to residual holdfasts; *C. grevillei, E. radiata* and *S. fallax.* A positive association seems apparent between the density of residual holdfasts and the total (rather than mean) abundance of recruits under denser but not sparse canopies (Fig. 4). No such significant relationship was detected by ANOVA: *C. grevillei* ($F_{1,20} = 2.82$, P > 0.05), *E. radiata* ($F_{1,20} = 0.01$, P > 0.05) and *S. fallax* ($F_{1,20} = 0.87$, P > 0.05). Again, this is likely



Fig. 4. Total abundance m^{-2} of particular recruits observed attached to holdfasts remaining on the substratum (striped bars) and relatively bare substratum (open bars) under dense and sparse canopies.

due to large variation in the number of recruits among plots. It is noteworthy that more experimental plots with dense canopies had greater total abundance of recruits on residual holdfasts than on barer substratum for *C. grevillei* (P < 0.05; Fisher's exact test), *E. radiata* (P < 0.05; Fisher's exact test) and *S. fallax* (P < 0.01; Fisher's exact test).

DISCUSSION

The richness of macroalgal species that recruited to disturbed areas of monospecific *E. radiata* was not solely dependant on decreases in canopy cover but also affected by the availability of barer substratum. This experimental evidence supports the model that the loss of established algae within monospecific

stands provides opportunities for the recruitment of alternate species of algae (Kirkman 1981; Reed & Foster 1984; Emmerson & Collings 1998; Wernberg-Møller 2002). Importantly, greater species richness in disturbed patches was neither a simple function of gaps created in the canopy nor free space on the substratum but due to a combination of both factors. The current study is unique in establishing this model for algae that form canopies rather than understorey species.

Patterns of recovery of algae following disturbance to adult forests are considerably variable across southern Australia. In New South Wales, re-establishment of the canopy by *E. radiata* only occurred when canopies were disturbed in Austral winter. Substrata in experimental clearings made at any other time of the year were dominated by turf-forming algae which may inhibit the recruitment of canopy-formers (Kennelly 1987a, c). In the current study, increases in the number of species of canopy-forming algae in patches of E. radiata disturbed in Austral spring are consistent with results from experimental clearings in Western and South Australia (Kirkman 1981; Emmerson & Collings 1998). This variability may be explained by differences in the timing of spore release among these biogeographic regions: over more of the year in the southern regions of Australia (Victoria, South and Western Australia) vs restricted to Austral winter in New South Wales (Steinberg & Kendrick 1999). Furthermore, associations between canopies of E. radiata and turf-forming algae in South Australia are different from those in New South Wales but more similar to Western Australia (Irving & Connell 2004). Our knowledge of the complex processes which govern the recovery of assemblages of algae following disturbance is not, as yet sufficient to make biogeographic comparisons. We therefore encourage further experimental work done at a number of spatial and temporal scales in Australian forests of kelp, to tease apart the relative and interactive effects of disturbance on the dynamics of both understorey as well as canopy species present as juveniles in the understorey.

In the current study, removing canopy caused greater species richness in the recruit assemblage only when barer space on the substratum was also freed (e.g. fewer residual holdfasts on the substratum). Studies in the northern hemisphere on similar assemblages of Laminarian algae indicate that juveniles of canopy-forming algae rarely establish under dense adult canopies (Rosenthal et al. 1974) because their growth is limited by the availability of light (Dayton et al. 1984; Edwards 1998). Other studies in Western and South Australia have observed substantial numbers of recruits of Cystophora and Sargassum species under adult canopies of the same species (Kendrick & Walker 1994; Hotchkiss 1999), hence light may not be the critical factor limiting the recruitment of canopy-forming algae in southern Australian forests. Although residual holdfasts may not persist for more than a year (Anderson et al. 1997), it is clear that canopy-forming algae are influenced by their presence in early stages of recruitment and establishment. These results highlight the need for awareness of the nature of the substratum when ascertaining the effects of canopies on the re-invasion of disturbed patches (e.g. Minchinton 2001).

Hay & South (1979) found that remnant holdfasts of Durvillea antartica (Chamisso) Hariot in experimentally cleared forests in New Zealand inhibited the recruitment of algae. Alternatively, a substantially greater abundance of juveniles of the South African species Ecklonia maxima (Osbeck) Papenfuss were found attached to holdfasts of adult plants than bare rock, particularly when there were many molluscan grazers (Anderson et al. 1997). Unlike the holdfasts of many Laminariales which have intertwining haptera, the holdfasts of Durvillea species are solid limiting the complexity of this structure. In the current study, juvenile macroalgae did establish under dense and sparse canopies of E. radiata, but the number of residual holdfasts was only important under dense canopies. Further, the greater abundance of recruits attached to residual holdfasts vs bare substrata suggests that the complexity in features of the substratum become important when the negative effects of canopies are exaggerated (as under dense canopies).

Complexity of substratum is important for the recruitment

and survival of plant propagules and their subsequent growth (Fletcher & Callow 1992). Increased complexity of substratum may allow juveniles to escape some of the negative influences of dense canopies which would normally inhibit the establishment and growth of juvenile algae. For example, in South Australian forests of *E. radiata* the substratum is generally covered by topographically smooth encrusting coralline algae (Fowler-Walker & Connell 2002) and is subject to continual abrasion by the adult fronds (Connell 2003). Crevices and increased sites for attachment in the intertwined haptera of holdfasts of *E. radiata* may provide protection from scour or predation which can be more intense under denser canopies (Bodkin 1988; Kennelly 1989; Connell 2003).

Forests of algae may be maintained by dormant stages of juvenile sporophytes or microscopic gametophytes; the marine equivalent of terrestrial 'seedbanks' allowing persistence in unstable conditions (Schiel 1985; Edwards 2000). Laminariales and Fucales both have long adult life-spans (Novaczek 1981; Clayton 1990): greater than 10 years, but it is unlikely that maximum age is ever reached because these plants are so often subject to disturbance (Steinberg & Kendrick 1999). The longevity of sporophytes in field conditions is unknown but spores of E. radiata are capable of growth following constant darkness for many months (Novaczek 1984). Furthermore, juveniles present underneath dense canopies of adults have been recorded for species of Cystophora (Hotchkiss 1999), Sargassum (Kendrick & Walker 1994) and E. radiata (Kirkman 1981; Andrew & Jones 1990). We acknowledge that the recruits in our study may not have arrived via dispersal but existed as a population of tiny understorey juveniles that were able to grow to form part of the canopy population following our manipulations. This possibility does not detract from the primary conclusion that thinning the canopy as well as increased space available on the substratum initiates greater diversity of recruits of canopy-forming algae. Further research will identify the stage(s) at which such recruitment is primarily affected by these types of disturbances.

Disturbance can modify the competitive interactions of species (Wilson & Keddy 1986) thereby influencing the composition of habitats. The expansive nature of the fronds and large holdfast of E. radiata allows the persistence of this species in monospecific arrays (Schiel 1988). It is clear, however, that this hierarchy (E. radiata vs fucalean algae) was not maintained for some months after disturbance. Because Fucalean algae can procure resources (space and light) more rapidly than E. radiata (Clayton 1990; Bolton & Anderson 1994), the conditions created by disturbance in the current study may facilitate a change in the competitive interactions (fucalean algae vs E. radiata) consistent with the competitive change hypothesis (Suding & Goldberg 2001). Although we do not infer that the greater diversity of recruits translates to greater diversity of adult canopies, we highlight the complex and interactive role that different attributes of disturbed patches play in initiating changes in the composition of these forests of algae.

Although it is possible to quantify changes in the structure of assemblages following disturbance (i.e. initiation), but defining whether such a state persists (i.e. the state initiated is maintained) is more difficult because it is extremely scale dependant (Petraitis & Latham 1999). Nevertheless, although local diversity (within patches) initiated by disturbance may not persist, regional diversity (among patches) can be maintained by asynchronous disturbance events in a number of patches; the landscape is a mosaic of different successional stages, each patch varying in composition (Thrush 1991; Sousa 2001). Disturbance events which are localised coupled with extreme variability in the kinds of disturbance and the damage done may explain much of the variability in the composition of algae at small spatial scales which is characteristic of forests of subtidal algae in Australia (Underwood et al. 1991; Goodsell et al. 2004). It is important to ascertain and separate processes that both initiate and maintain diversity (Petraitis & Latham 1999) and further research is needed to understand the mechanisms of succession and the interactions among adult species (e.g. Benedetti-Cecchi & Cinelli 1993) to understand the long term effects of disturbance in forest of E. radiata.

In conclusion, high productivity and biomass of forests of canopy-forming algae make these habitats important components of coastal systems in temperate Australia (Walker & Kendrick 1998). Substantial small-scale variation in species composition of these forests has important consequences for understorey species of algae (Irving & Connell 2004) and animals that rely on them as habitat (Goodsell *et al.* 2004). Understanding the dynamics of assemblages of algae provides the basis for an understanding of the ecology of this habitat that dominates so much space and has strong influence on subtidal assemblages of rocky coastlines in temperate Australia.

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