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Physical disturbance and subtidal habitat structure on open rocky coasts: Effects of wave exposure, extent and intensity

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Abstract

Canopy-forming algae occur across of range of energy environments (i.e., wave sheltered to exposed coasts) where disturbances are frequent (i.e., gap formation) and benthic patterns largely reflect variation in post-disturbance processes. Disturbances vary in extent (area affected) and intensity (degree of damage), and this may affect recolonisation at local scales. On an open oceanic coast, we tested whether habitat structure (patches of canopy algae) differed between heavy and relatively lighter wave exposure (sheltered vs. exposed sides of islands), and whether wave exposure affected the response of prominent habitat-formers to varying disturbance regimes (different sizes of partial and complete canopy removal). Observations of naturally occurring patterns showed sheltered coasts to be characterised by small patches of fucoids, whereas exposed coasts were characterised by large patches of kelp. Canopy-gaps were larger at exposed than sheltered coasts, and mixed canopies constituted >24% of the subtidal rocky habitat independently of wave exposure. Experimental disturbances showed the local density of kelps to affect recovery through greater recruitment to partial clearings (80% canopy removal). Fucalean algae, on the other hand, mainly recruited into complete clearings (100% removal), but when their recruits were abundant, they also recruited into partial clearings. The covers of filamentous, turf-forming algae increased in all clearings, and more so at exposed than sheltered sites. Extent of disturbance had no detectable effect on recolonisation by canopy-forming algae across the scales examined (i.e., 1.5 m, 3 m diameter loss of canopy). Recolonisation varied among islands kilometres apart, and correlations ($r > 0.85$) between cover of canopies and cover of their recruits in clearings at the scale of sites, suggested that differences in propagule supply could account for variation in patterns of recolonisation at scales of kilometres. There was no evidence to suggest that the effect of disturbance depended on wave exposure within the range of exposures tested in this study (i.e. open coasts). We recognise that wave exposure can be fundamental to habitat structure of subtidal rocky coasts, but we suggest that its influence may be mediated by the biological setting (e.g., canopy composition).

Keywords: Disturbance regime; Kelp forest ecology; Habitat heterogeneity; Wave exposure; Subtidal canopy algae

1. Introduction

On temperate rocky coasts, the predominant habitats (macroalgae) represent naturally disturbed systems (Witman and Dayton, 2001) where the spatial patterns may largely reflect variation in post-disturbance recovery (Connell, 2007). Disturbances are discrete events that

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destroy biomass (Grime, 1977) in variable amounts, i.e. the spatial extent (area affected) and intensity (degree of damage) of disturbances vary. In forest habitats (e.g., boreal forests and kelp forests) disturbances range from pruning, where only parts of plants are lost (Kennelly, 1987a; Nagel and Diaci, 2006), through loss of whole plants and clumps of plants (Kennelly, 1987a; Seymour et al., 1989; Nagel and Diaci, 2006), to catastrophic events where extensive areas are denuded (Dayton and Tegner, 1984; Clinton and Baker, 2000; Edwards and Estes, 2006).

Extent and intensity are fundamental properties of physical disturbances because local processes (e.g. recruitment, predation and amelioration of the physical environment) are mediated by canopy density over restricted spatial scales (e.g., Reed et al., 1988; Petraitis and Dudgeon, 1999; McLaren and Jefferies, 2004; Wernberg et al., 2005). The extent and intensity of disturbances, therefore, shape the trajectory of post-disturbance recovery across a range of habitats (e.g., terrestrial hardwood, Castleberry et al., 2000; and rocky shores, Sousa, 1984; Dudgeon and Petraitis, 2001; Speidel et al., 2001), including macroalgal forests in the southern (Goodsell and Connell, 2005) and northern (Wernberg, 2006) hemispheres. What is often missing, however, from our understanding of forest ecology is whether extent and intensity act as separate and independent properties of disturbances, or act as synergistic and interdependent forces.

Waves are a common source of disturbance on rocky coasts (e.g., Paine and Levin, 1981; Seymour et al., 1989). In addition to the strong direct effects of disturbances, waves also have indirect effects on community structure through influencing dispersal patterns, ecological interactions and how canopy algae modify environmental conditions. For example, waves extend the effective dispersal distance of propagules from canopy-forming algae considerably (Reed et al., 1988; Gaylord et al., 2002) and they influence the vigour of canopy sweeping (Kennelly, 1989). Sweeping, in turn, modify sediment accumulation (Kennelly, 1989) and light levels (Gerard, 1984) in the understorey, which may affect organisms living there (Wernberg et al., 2005). Abrasion from sweeping fronds also affect the recruitment, survival and growth of understorey algae and invertebrates (Connell, 2003b) and it can prevent consumers from accessing prey living within reach of the canopy fronds (Gagnon et al., 2003a,b). Since waves modify key ecological processes that influence post-disturbance colonisation and recovery (dispersal distances, sweeping), the effects of extent and intensity of disturbances likely depends on the degree of wave exposure.

Rocky coasts throughout temperate Australia are dominated by a low canopy of the small kelp *Ecklonia radiata* and various fucalean algae, mainly from the genera *Cystophora*, *Phyllospora*, *Sargassum* and *Scytothalia* (Wernberg et al., 2003; Goldberg and Kendrick, 2004; Goodsell et al., 2004; Connell and Irving, 2008). Canopy composition varies spatially (Connell and Irving, 2008); some places are characterised by monospecific beds of *E. radiata* (Kendrick et al., 1999), or various species of fucoids (Collings and Cheshire, 1998; Turner and Cheshire, 2003) and other places have a mixed canopy (Goodsell et al., 2004). Wave exposure can affect canopy composition (Turner and Cheshire, 2003; Goldberg and Kendrick, 2004), and these effects may be mediated by species-specific tolerances to physiological and mechanical constraints such as nutrient uptake kinetics in stagnant water, and dislodgment in turbulent water (see reviews in Hurd, 2000; Thomsen and Wernberg, 2005), or ecological interactions that could themselves be influenced by canopies and waves (e.g., consumption, Gagnon et al., 2003a,b).

We investigate whether wave exposure interacts with the disturbance regime (extent and intensity of disturbances) to create mosaics of patches dominated by different canopy algae on subtidal rocky coasts. Specifically, we test the hypotheses that 1) canopy types and their patch sizes differ between wave exposed and sheltered rock, and that 2) post-disturbance colonisation of benthos, and recolonisation of canopy-forming algae, depends on the extent and intensity of disturbances, and that 3) wave exposure affects the responses of these habitats to disturbances of different extent and intensity.

2. Materials and methods

2.1. Study sites

These hypotheses (above) were tested through observation and experimentation on the open oceanic coast of Encounter Bay (South Australia). Three offshore granite islands (Fig. 1) provide the conditions needed to study wave exposure; i.e. offshore sides are fully exposed to swells from the Southern Ocean, and the inshore sides are less exposed. We quantified patterns of canopy configuration at six sites; the exposed and sheltered sides of three islands (West Island, Wright Island and Seal Rocks = WE, WI, SR), and experimentally assessed effects of disturbance at four sites; the exposed and sheltered sides of two islands (WI, SR). In addition to known differences in wave height and water velocities among these sites (Fowler-Walker et al., 2006), we also calculated Baardseth's wave exposure index (range: 0–36, higher values indicating higher wave exposure) for each of the six sites by counting the number of 9° sectors open to > 7.5 km fetch

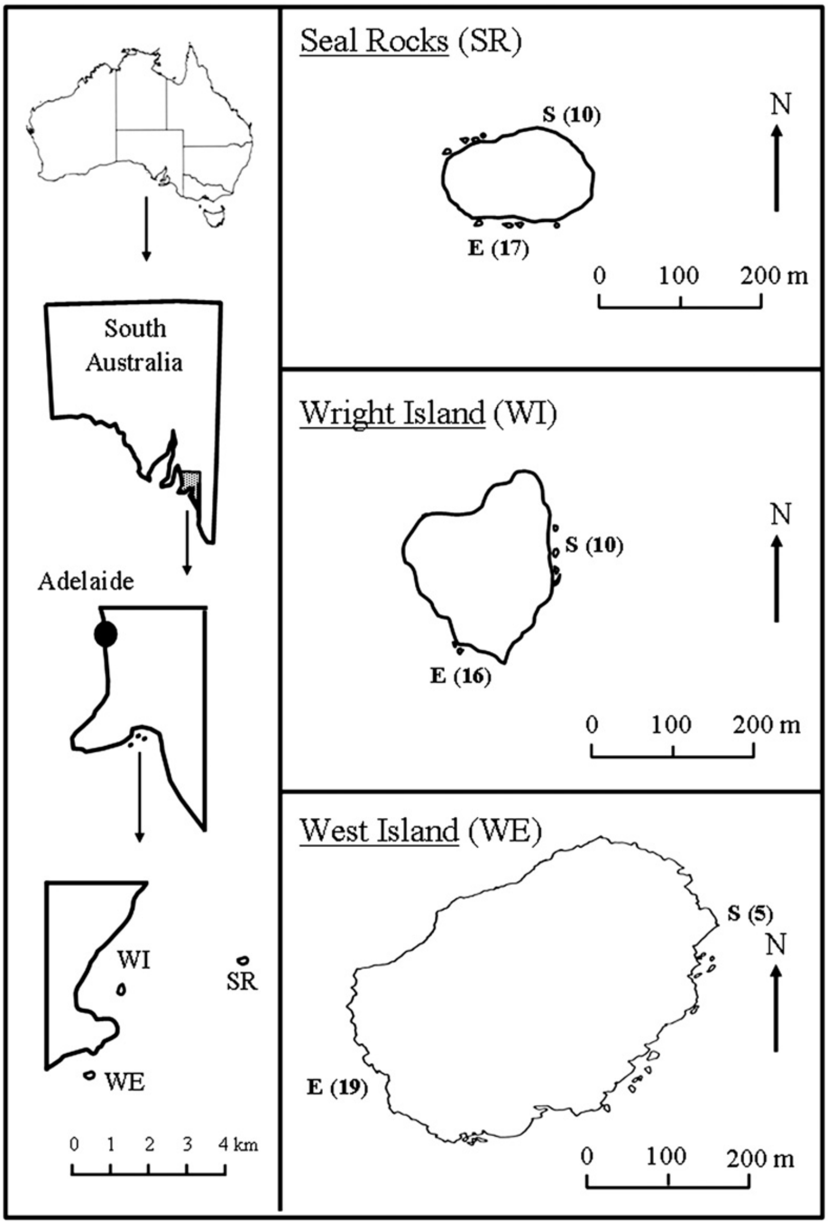

Fig. 1. Location of sheltered (S) and exposed (E) study sites at Seal Rocks (S 35°34'36'' E 138°38'39''), Wright Island (S 35°34'58'' E 138°36'32'') and West Island (S 35°36'21'' E 138°35'31'') within Encounter Bay, South Australia. Baardseth's exposure index is given in parenthesis for each site.

(Baardseth, 1970). A paired *t*-test was used to test whether offshore sides of the islands were more exposed (i.e., had higher index values) than inshore sides.

2.2. Habitat structure

We tested for an association between wave exposure and habitat structure by quantifying canopy composition and patch size at exposed and sheltered sides of the three islands. Habitat structure was quantified along four 100 m transects set perpendicular to the coastline at each site. Transects were separated by at least 20 m and started at ~1.5 m depth, stopping only if the end of the rocky slope was reached (8–12 m depth). We used the approach of Goodsell et al. (2004), where canopy patches >~1 m were recognised; swimming along the transect line a diver recorded the start and end of individual habitat patches intersecting the transect line to the nearest 10 cm. We focused on four broadly defined habitat types: mono-specific kelp (canopy >80% *E. radiata*), fucalean algae (canopy >80% of the genera *Cystophora*, *Sargassum* and *Scytothalia*), mixed kelp and fucalean algae (canopy of kelp and fucalean algae growing interspersed <1 m apart), and open gaps without canopy cover (usually covered by filamentous algae or small foliose algae). These four habitat categories were selected because they represent functionally meaningful units. For example, reproductive ecology and canopy morphology differs systematically between kelp and fucalean algae (Schiel and Foster, 2006). Similarly, environmental conditions such as light, sediment levels and abrasion differ between the understories of kelp, mixed and open patches (Wernberg et al., 2005; Irving and Connell, 2006), which are also characterised by different assemblages of algae and invertebrates (Kendrick et al., 1999; Turner and Cheshire, 2003; Irving et al., 2004b; Irving and Connell, 2006).

The relative canopy composition at each site was calculated as the mean percentage of each transect covered by each patch type, and differences between wave exposures (fixed factor) and among islands (random factor) were tested with a mixed model two-way ANOVA, followed by SNK-tests for pair-wise comparisons.

The one-dimensional size of individual patches was determined by measuring the beginning and end of each patch intersecting the transect line. Patches of each habitat type were pooled within exposed and sheltered sites across islands to provide a more powerful test for differences in patch characteristics between exposed and sheltered environments. Subsequently, a Kolmogorov–Smirnov test for continuous data was used to test if the size frequency distribution of each patch type was different between exposed and sheltered rock.

2.3. Effects of disturbances

We experimentally tested the interactive effects of wave exposure, extent of disturbance and intensity of disturbance on recruitment of canopy-forming algae and dominant habitat formers. We manipulated physical disturbances by creating circular clearings in the canopy cover of *E. radiata*. Mixed canopies were found at all sites, but we placed the centre of each clearing within a patch of mono-specific kelp no smaller than 1 m^2. This was done to ensure that all areas to be sampled at the end of the experiment had a similar history. To coincide with the timing of winter storms, the prevalent source of physical disturbances, the experiment was set up in July 2004 and sampled 8 months later in March 2005, just prior to the beginning of next winter. Percent cover was used to quantify the abundance of habitat formers because it is a commonly used, ecologically relevant (pre-emption of space) metric which is commensurable across differently shaped and sized taxa. The percentage cover of *E. radiata* recruits, fucoid recruits, filamentous algae, encrusting algae, foliose algae and sessile animals was quantified in the centre of each experimental plot using the point intercept method (20 × 20 cm quadrat with 25 intersections, Drummond and Connell, 2005). The experiment was set up at 7–10 m depth at two islands (WI, SR; random factor) and adopted a fully orthogonal design with wave exposure (fixed factor, 2 levels: exposed, sheltered = E, S), disturbance extent (fixed factor, 3 levels: 0 m, 1.5 m and 3.0 m diameter [1.8 m^2 and 7.1 m^2] = N, S, L) and disturbance intensity (fixed factor, 2 levels: complete and partial canopy removal [~20% of ambient canopy density remaining] = C, P). The first level of the extent factor (N = no canopy clearing) was effectively a control treatment where the canopy was left intact. Each treatment was replicated five times at each site. Data from the experiment was analysed with mixed model four-factor ANOVA followed by SNK tests for pair-wise comparisons.

Pearsons correlation was used to test if there was a relationship between the percent cover of *Ecklonia* or fucalean algae at each site, and the percentage cover of their recruits averaged across across all experimental disturbances ($n=4$ sites). When estimating the total cover of *Ecklonia* and fucoids, ‘mixed canopies’ were assumed to represent 50% of each of these canopy types.

3. Results

3.1. Wave exposure

Baardseth's wave exposure index was significantly higher ($t=-4.49$, $p=0.046$) for the exposed offshore sides of the islands than for the sheltered inshore sides (exposed 17.3 ± 0.9 SE, sheltered 9.0 ± 1.0, $n=3$). Concurrent observations showed sheltered coasts to have 25–36% lower wave heights and 38–42% lower maximum water velocities at 8 m depth, than exposed coasts at Seal Rocks and Wright Island (Fowler-Walker et al., 2006).

3.2. Habitat structure

The exposed sides of the islands had a significantly higher cover of kelp ($MS_{(exp)}=9660.0$, $F_{(1,2)}=70.9$, $p=0.014$) and a lower cover of fucalean algae ($Ln(x+1)$-transformed, $MS_{(exp)}=27.3$, $F_{(1,2)}=128.7$, $p=0.008$) than the sheltered sides. The cover of kelp canopies ranged from 52–77% of the rock at exposed sides of the islands to 3–43% at sheltered sides (Fig. 2). Conversely, fucoid canopies covered from 0–16% to 15–50% of the habitat at exposed and sheltered rock respectively (Fig. 2). These effects of wave exposure were consistent ($p_{is \times exp}>0.55$) regardless of differences among islands for both kelp ($MS_{(is)}=2398.9$, $F_{(2,18)}=11.0$, $p=0.001$, SNK: WE = WI < SR) and fucalean algae ($Ln(x+1)$-

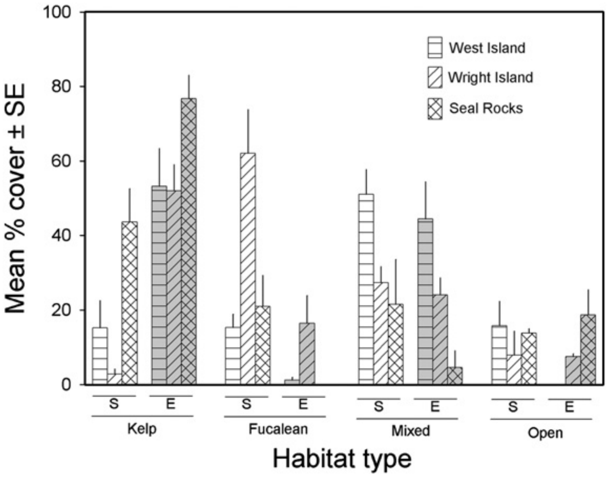

Fig. 2. Mean percentage cover + SE ($n = 4$ transects per site) of habitat types among sheltered (S) and exposed (E) sides of three islands in Encounter Bay.

transformed, $MS_{(is)} = 8.1$, $F_{(2,18)} = 7.6$, $p = 0.004$, SNK: WE = SR < WI). Wave exposure had no effect ($p > 0.11$) on the cover of mixed canopies (5–51%) or open gaps (0–19%) (Fig. 2).

All habitat types were found as patches covering a range of sizes up to 10 m or more (Fig. 3). Mean patch sizes ranged between 3.3 and 13.7 m (Fig. 3), where kelp patches on exposed coasts (13.7 m) were considerably larger than patches of all other canopy types anywhere (3.3–5.2 m). Wave exposure had a significant effect on the patch size frequency distribution of kelp ($D_{max} = 0.50$, $p < 0.001$) and open gaps ($D_{max} = 0.49$, $p < 0.005$), where patch sizes of sheltered coasts were skewed towards smaller patches relative to exposed coasts (Fig. 3). Patches of kelp canopy covered the largest range of sizes, up to 53.5 m on exposed coasts. In contrast, patches of fucalean canopy were small (<9.3 m) and much more abundant on sheltered compared to exposed coasts (Fig. 3). Wave exposure did not have any effect on the size distribution of patches of fucalean canopy ($D_{max} = 0.27$, $p > 0.2$). Patches of mixed canopies were almost twice as abundant on sheltered as on exposed coasts, but their size-frequency distributions did not differ between wave exposures ($D_{max} = 0.15$, $p > 0.1$) and maximum patch sizes were ~20 m regardless of wave exposure. Sheltered coasts had more, but smaller, open gaps than exposed coasts where the largest gap found was 19 m.

3.3. Effects of disturbances

Recruitment of *Ecklonia* into clearings varied between the two islands (Fig. 4; Table 1a). Canopy clearings at Seal Rocks had higher covers of kelp recruits (2.4–24%) than uncleared control plots (<2.4%) regardless of

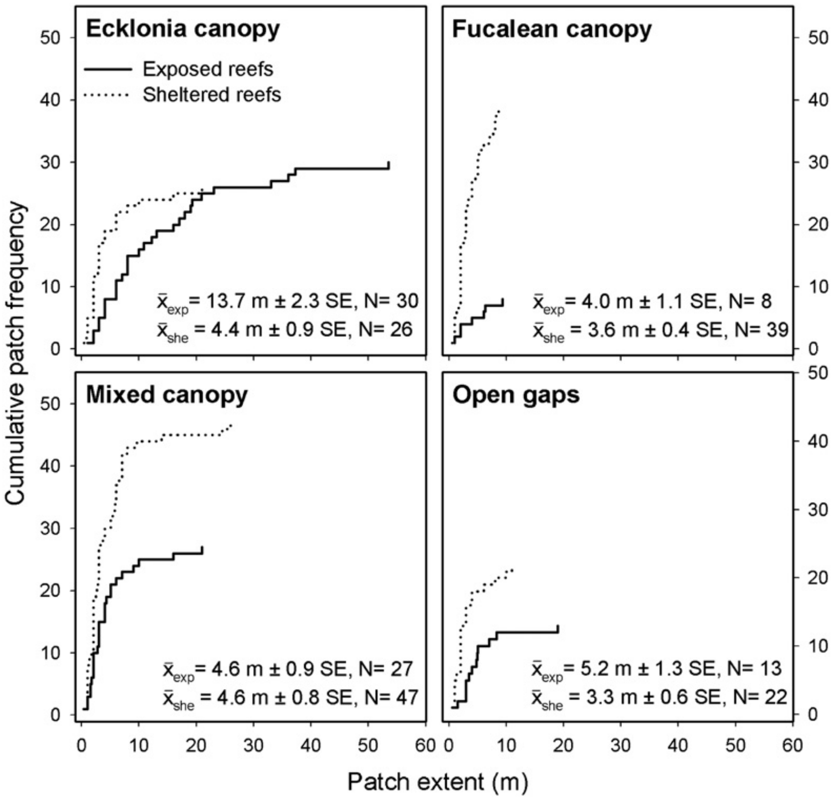

Fig. 3. Cumulative size frequencies of habitat patches at exposed (exp) and sheltered (she) sites pooled across three islands in Encounter Bay. Values listed are mean patch sizes (±SE) and total number of patches (N).

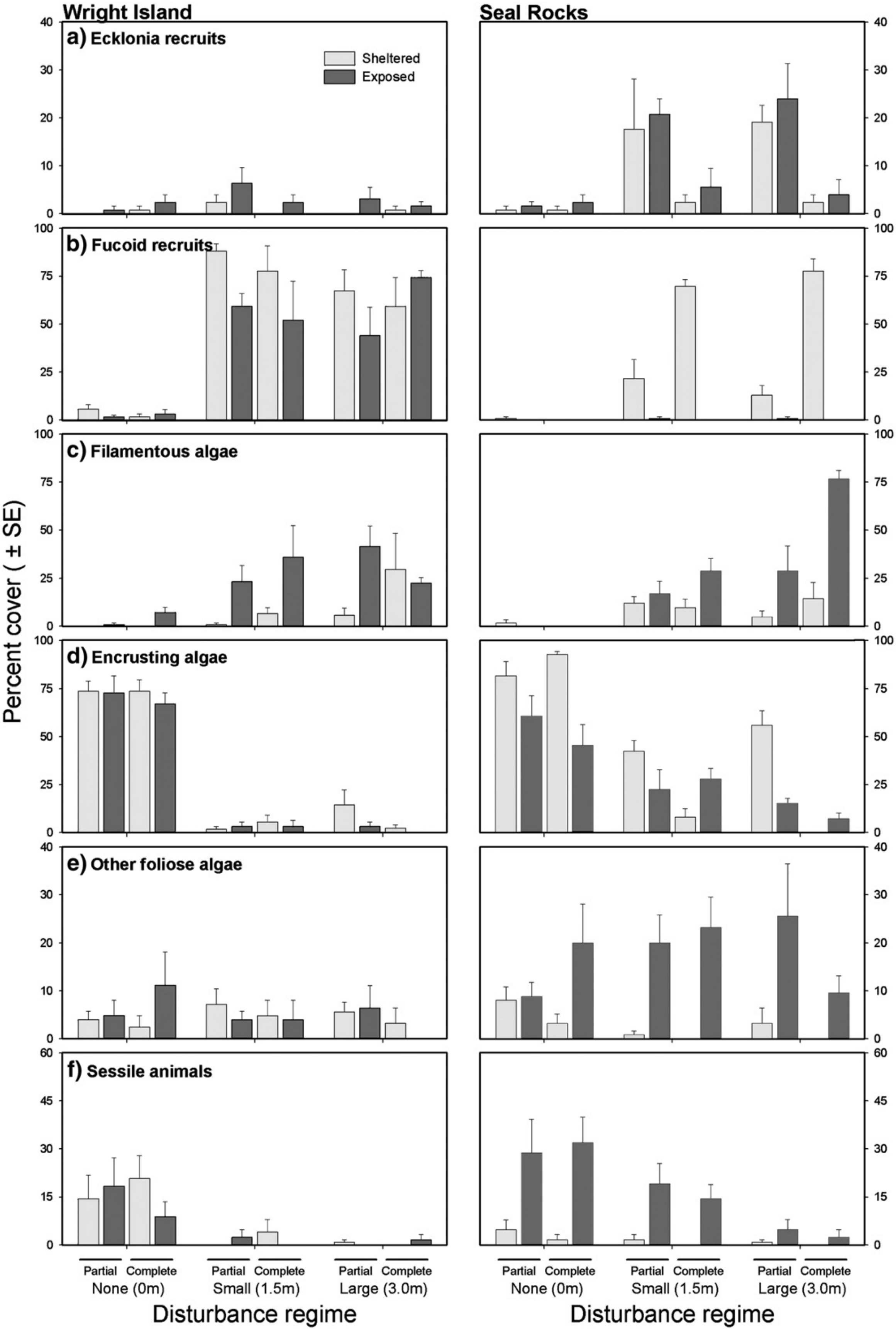

Fig. 4. Mean percentage cover +SE ($n=5$ clearings per treatment per site) of dominant assemblage-formers 8 months after canopies were cleared at variable intensities (partial vs. complete clearance) and extents (none vs. small vs. large) at sheltered and exposed sites.

Table 1

Results of four-factor ANOVA testing for differences in abundance of habitat formers among islands (Is), exposure (Exp), clearing intensity (In) and extent (Ext)

Source of variation	*df*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
		a) Kelp recruits			*b) Fucoid recruits*			*c) Filamentous algae*			*d) Encrusting algae*			*e) Other foliose algae*			*f) Sessile animals*		
Transformation and Cochran's test		Ln(x+1); C=0.15; p>0.05			Ln(x+1); C=0.20; $p<0.05^{a}$			Ln(x+1); C=0.17; p>0.05			None; C=0.14; p>0.05			Ln(x+1); C=0.09; p>0.05			Ln(x+1); C=0.12; p>0.05		
Islands	1	22.09	24.0	**0.000**	89.22	97.5	**0.000**	0.07	0.1	0.795	4037	23.8	**0.000**	11.33	9.5	**0.003**	4.29	4.0	**0.048**
Exposure	1	9.93	43.7	0.096	43.51	1.9	0.403	45.93	9.8	0.197	3162	2.4	0.367	26.02	0.7	0.547	19.96	0.8	0.547
Intensity	1	12.8	1.3	0.456	0.49	0.1	0.819	8.17	145.5	0.053	2689	2.0	0.391	5.44	11.8	0.181	0.37	0.4	0.645
Extent	2	7.75	1.8	0.356	73.02	10.1	0.090	55.0	30.1	**0.032**	44430	30.9	**0.031**	1.43	6.2	0.138	32.21	8.6	0.105
Is × Exp	1	0.16	0.2	0.679	23.46	25.6	**0.000**	4.70	4.2	**0.043**	1333	7.9	**0.006**	35.00	29.5	**0.000**	26.77	25.0	**0.000**
Is × In	1	9.73	10.6	**0.002**	5.70	6.2	0.014	0.06	0.1	0.823	1333	7.9	**0.006**	0.46	0.4	0.534	0.94	0.9	0.352
Is × Ext	2	4.29	4.7	**0.012**	7.21	7.9	**0.001**	1.86	1.7	0.193	1436	8.5	**0.000**	0.23	0.2	0.824	3.76	3.5	**0.034**
Exp × In	1	0.21	4.8	0.274	1.65	0.2	0.741	0.33	0.2	0.764	770	1.0	0.508	1.94	17.4	0.150	0.32	0.2	0.764
Exp × Ext	2	0.39	2.2	0.310	8.55	1.3	0.434	5.32	3.3	0.235	883	1.4	0.410	0.70	0.1	0.876	1.78	0.5	0.673
In × Ext	2	5.74	2.4	0.298	1.56	1.5	0.405	1.16	0.4	0.717	837	2.0	0.331	2.13	15.5	0.061	0.06	1.8	0.364
Is × Exp × In	1	0.05	0.1	0.825	8.86	9.7	**0.003**	2.18	2.0	0.164	811	4.8	**0.031**	0.11	0.1	0.760	2.11	2.0	0.163
Is × Exp × Ext	2	0.18	0.2	0.828	6.56	7.2	**0.001**	1.64	1.5	0.234	614	3.6	**0.031**	4.93	4.2	**0.019**	3.67	3.4	**0.037**
Is × In × Ext	2	2.44	2.6	0.076	1.07	1.2	0.316	2.94	2.7	0.076	415	2.5	0.092	0.14	0.1	0.891	0.04	0.0	0.967
Exp × In × Ext	2	0.16	0.5	0.689	3.56	1.9	0.347	1.49	0.7	0.581	1348	1.7	0.377	2.32	10.6	0.087	0.47	0.2	0.821
Is × Exp × In × Ext	2	0.36	0.4	0.679	1.89	2.1	0.132	2.07	1.9	0.161	815	4.8	**0.010**	0.22	0.2	0.832	2.17	2.0	0.137
Residual	96	0.92			0.92			1.11			170			1.19			1.07		

p-values considered significant are highlighted in bold.

[a] Not possible to equalise variances by transformation. Significance determined at $p<0.01$.

the size of clearing (SNK_{SR}: N<S=L). Furthermore, partial clearings had considerably higher covers of kelp recruits (18–24%) than complete clearings at Seal Rocks (2.4–5%) (SNK_{SR}: C<P). In contrast, the cover of kelp recruits was very low (<10%) in all treatments at Wright Island, and none of the disturbance treatments had a significant effect (SNK_{WI}: N=S=L; C=P). Despite this lack of significance, however, mean kelp recruit abundances showed similar patterns to those at Seal Rocks across both wave exposure and clearing intensity. There was no difference in the cover of kelp recruits between islands in control plots (SNK_{N}: WI=SR) and wave exposure did not influence the response of kelp recruits to canopy clearing.

Recruitment of fucalean algae also differed between the two islands (Fig. 4; Table 1b). There was an interaction among islands, clearing intensity and wave exposure: at Wright Island both partial and complete canopy clearings always had greater covers (44–88%) of fucoid recruits than uncleared controls (<5.6%) (SNK_{WI}: N<S=L) regardless of wave exposure (SNK_{WI}: S=E) and clearing intensity (SNK_{WI}: C=P). At Seal Rocks, on the other hand, fucoids only recruited into clearings on the sheltered side (SNK_{SR}: S>E) and in considerably higher densities in complete (67–78%) compared to partial (13–22%) clearings (SNK_{SR}: C>P). There was no difference between Wright Island and Seal Rocks in the cover of fucoid recruits in control plots (SNK_{N}: WI=SR).

There were positive correlations between the cover of adult canopy formers in the surrounding habitat (cf. habitat structure) and the cover of their recruits in clearings at the experimental sites ($n=4$) for both kelp ($r=0.95$) and fucalean algae ($r=0.85$).

Disturbance had a positive effect on the percentage cover of filamentous algae (Fig. 4; Table 1c) in clearings (N<0.3%, S, L>0.8–42%; SNK: N<S=L). The exposed sites had consistently greater percentage cover of filamentous algae than the sheltered sites (E<77%, S<30%) (SNK: S<E) although the magnitude of the effect varied between islands. Clearing intensity had a near-significant effect ($p=0.05$) on the cover of filamentous algae such that complete clearings usually had higher covers of filamentous algae than partial clearings (Fig. 4).

The experimental effects on the cover of encrusting algae were complex with several significant higher-order interactions (Fig. 4; Table 1d). In general, the cover of encrusting algae was smaller in clearings (0–56%) than under canopy (46–93%). In most cases, the size of clearing was not important (7 of 8 SNKs: N>S=L), and when it was, large clearings had less cover of encrusting algae than small clearings (1 SNK: N>S>L). Intensity of disturbance generally did not have an effect on the percent cover of encrusting algae (10 of 12 SNKs: C=P), and when it did, complete clearings had lower covers of crusts than partial clearings (2 SNK: C<P). Wave exposure did affect the cover of encrusting algae, but the effects were variable with no unequivocal patterns of direction (Fig. 4).

The responses of other foliose algae (Table 1e) and sessile animals (Table 1f) to the experimental treatments were characterised by a significant interaction between islands, exposure and extent of clearing. There were no effects on foliose algae at Wright Island and their cover varied inconsistently between 2.4 and 11% among experimental treatments (Fig. 4). The exposed side of Seal Rocks had significantly higher cover (~20%) of foliose algae than the sheltered side (<8%). Nevertheless, control plots had higher covers of foliose algae at the sheltered side of Seal Rocks (3.2–8%) than canopy clearings (0–3.2%) ($SNK_{SR,S}$: N>S=L).

Wave exposure had no effect on the percentage cover of sessile animals at Wright Island (SNK_{WI}: S=E). Canopy clearings had a sparser cover of sessile animals than control plots (<4% *vs.* 9–21%) regardless of extent of disturbance (SNK_{WI}: N>S=L). In contrast, there was a large difference in the percentage cover of sessile animals on the sheltered and exposed side of Seal Rocks (SNK_{SR}: S<E). At the exposed side of Seal Rocks, where sessile animals were abundant (2.4–32%), the effect of disturbance was a lower cover as seen at Wright Island, although only large clearings had a lower cover (SNK_{SR}: N=S>L). Disturbance did however not have any effect ($SNK_{SR,S}$: N=S=L; P=C) on the cover of sessile animals at the sheltered side of Seal Rocks, where there were very few sessile animals (<4.8%). Clearing intensity did not have any effects on the cover of other foliose algae or sessile invertebrates.

4. Discussion

Habitat structure differed between exposed and sheltered sides of islands and post-disturbance cover of habitat often, but not always, was affected by wave exposure and spatial extent and intensity of disturbance. There was no evidence to suggest that the effect of disturbance depended on wave exposure. Variation in canopy composition and experimental responses among islands suggested that many experimental effects could have been influenced by surrounding canopy composition.

4.1. Habitat structure

That habitats occur as mosaics is frequently emphasized as a characteristic of intertidal and subtidal rocky coasts (e.g., Paine and Levin 1981; Menge et al., 1993;

Wernberg, 2006; Connell and Irving, 2008). Physical disturbance from waves is often thought to explain the origin of this heterogeneity, and of the few studies that have quantified the composition and sizes of mosaics, most have quantified gaps within the matrix of a habitat former (usually mussels or algae) in order to make statements about the disturbance regime (e.g., Paine and Levin, 1981; Kennelly, 1987a; Farrell, 1989; Wernberg, 2006). However, as demonstrated, the matrix of the habitat former can itself be patchy (i.e., different canopy algae) with individual habitat patches reaching in excess of 50 m, but with most <10 m.

Patches of kelp, fucoids and open gaps were found at both sheltered and exposed coasts. Sheltered coasts were dominated by many small patches of fucoids whereas exposed coasts were dominated by large kelp patches. Other studies from the south coast of Australia have also found *Ecklonia* to be more abundant than fucoids at relatively exposed sites (Shepherd and Womersley, 1970; Turner and Cheshire, 2003; Goldberg and Kendrick, 2004). Although wave exposure may determine the proportion of mono-specific stands, a general feature was that mixed stands, where kelps and fucoids grow interspersed <1 m apart, occupy a high proportion (>24%) of the rocky habitat regardless of wave exposure. Environmental conditions and ecological processes unique to either mono-specific or mixed habitats drive differences in their associated flora (Irving and Connell, 2006) and fauna (Goodsell and Connell, 2008). That the mixed canopy habitat is a characteristic feature across the geographic extent of the south coast of Australia (Goodsell et al., 2004; Connell and Irving, 2008) regardless of wave exposure (this study) is an important realisation that sets the ecology of the south coast apart from the temperate parts of the east and west coasts, where mono-specific canopies dominate (Wernberg et al., 2003; Connell and Irving, 2008).

The sizes of open gaps and kelp patches were larger on exposed relative to sheltered coasts. For gaps, this probably reflects that higher drag forces at exposed sites (Eckman et al., 2003; Fowler-Walker et al., 2006) causes more frequent dislodgment of canopy algae. Also, at exposed sites, many *Ecklonia* aggregate in clumps with fused holdfasts (Wernberg, 2005), so when dislodgment occurs, it is likely to be extensive with loss of clumps of individuals. As implied by the low abundance of canopy-recruits in complete clearings on exposed coasts, once formed, gaps exceeding 1–2 m may either persist or have delayed recovery (Wernberg, 2003, 2006, this study), thus increasing the relative frequency and extent of gaps. The predominance of large kelp patches on exposed coasts, on the other hand, could reflect a rapid infilling of small (<1 m) and partially disturbed areas as suggested by the high abundances of kelp recruits in experimental plots of partial canopy loss (i.e., Seal Rocks).

4.2. Disturbance regime

The responses of dominant assemblage formers to canopy clearings of different extent and intensity, varied among taxa. There was a lack of consistency in responses between the two islands, and there was no evidence to suggest that the magnitude or direction of responses were affected by wave exposure.

Studies from marine and terrestrial environments have demonstrated that the identity of recruiting organisms may depend on features of the disturbance regime such as the extent and intensity of the impact (e.g., Sousa, 1984; Castleberry et al., 2000; Dudgeon and Petraitis, 2001; Wernberg, 2006). The spatial extent and intensity of our experimental disturbances covered the low to mid range of naturally occurring gaps (Kennelly, 1987a; Connell and Irving, 2008, this study). The general lack of differences between small and large clearings therefore suggest that the processes controlling post-disturbance recolonisation (e.g., dispersal and recruitment) either are scale-invariant or operate at larger spatial scales such that larger clearings (>3 m diameter) are needed to demonstrate scale-dependent effects. Similarly, the lack of effect of our manipulation of disturbance intensity (i.e., thinning *vs.* complete removal), where environmental conditions such as light and frond abrasion likely differ (Fletcher and Day, 1983; Wernberg et al., 2005), suggests that these conditions play a subordinate role in determining recolonisation of the clearings.

Widespread recruitment of canopy-formers following disturbances is a ubiquitous feature of canopy-dominated habitats (e.g., Edwards, 1998; Dudgeon and Petraitis, 2001; Goodsell and Connell, 2005; Goldberg, 2007). Kelp and fucoid canopy-recruits showed markedly different responses to the imposed disturbance regimes. Kelp recruits were found at both islands, but only at Seal Rocks were disturbances followed by an increase in their abundance. Here, the increase was confined to the partial canopy clearings where the response was virtually identical at sheltered and exposed sites. Others have also found the abundance of *Ecklonia* recruits to be highly variable across sites separated by kilometres (Hatcher, 1989; Wernberg, 2003), suggesting that kilometre-scale processes such as site-specific differences in reproduction, propagule supply, nutrients, herbivory or the physical environment can sometimes decouple the otherwise strong effects of metre-scale processes associated with physical disturbances. Nevertheless, our experiment suggest that, at sites where *Ecklonia* does recruit, the survival of some adult plants may facilitate the recovery of the canopy following physical disturbances, irrespective of wave exposure and the spatial extent of the impact.

Unlike kelp, disturbances led to increased abundance of fucoid recruits at both islands. However, fucoid recruit densities were unaffected by disturbance regime or wave exposure at Wright Island, whereas the effect of intensity was strong at the sheltered side of Seal Rocks. There was virtually no recruitment of fucoids at the exposed side of Seal Rocks. Wave exposure can affect recruitment and recruit survival adversely; no direct comparison of fucoid and kelp recruits exist, but fucoids may require low water motion for successful reproduction (Serrao et al., 1996) or be relatively sensitive to mechanical stress from water motion (Taylor and Schiel, 2003). Kelp recruits, in contrast, may be more robust; calculations have shown that dislodgment forces of *Ecklonia* recruits are 2–5 times greater than the drag forces they normally encounter in exposed shallow subtidal environments (Thomsen et al., 2004). However, the relatively strong recruitment of fucoids at the exposed side of Wright Island suggests that wave exposure in itself is not a barrier to fucoid recruits, and therefore does not explain the absence of fucoid recruits at the exposed side of Seal Rocks. The strong correlations between the abundance of adult canopy formers at a site, and the abundance of their recruits in the experimental clearings of that site, suggest that a sizeable amount of the differences seen in the responses of recruits could reflect broad-scale patterns of propagule supply rather than inconsistencies in the ecological processes (Menge et al., 1993).

Canopy-forming algae facilitate encrusting algae, and suppress the growth of erect algae (Connell, 2003a). Consequently, loss of canopies cause an increase in the abundance of filamentous algae and a concomitant decrease in cover of encrusting algae (Kennelly, 1987b; Edwards, 1998; Wernberg, 2006). These effects were also observed at both islands in Encounter Bay, but while the effects on filamentous algae were relatively simple and consistent, effects on encrusting algae were characterised by complex interactions. Although canopy loss can have almost instantaneous adverse effects on the physiology of encrusting algae (Irving et al., 2004a), they can often recover from these effects and tolerate even persistent cover of turf (Airoldi, 1998; Figueiredo et al., 2000). Negative changes in cover of encrusting algae may therefore reflect over-growth by other species rather than an actual decrease in the abundance of crusts. As such, the complex interactive effects detected likely reflect that the response of encrusting algae integrates the responses of other assemblage components. The growth and monopolisation of space by filamentous algae, in contrast, can be very rapid (Connell, 2005; Wernberg, 2006).

4.3. Wave exposure

Wave exposure is generally considered one of the major environmental drivers of community structure in coastal environments (e.g., Menge et al., 1993; Goldberg and Kendrick, 2004; Lindegarth and Gamfeldt, 2005). Wave exposure is a complicated concept in an ecological context because waves and water motion affects almost every possible physical property of the environment including light, oxygen, sediment movement, and nutrient availability. Many of these physical factors are known to directly control physiological and ecological processes (Hurd, 2000). Consequently, there is an enormous scope for wave exposure to interact with, and compound the effects of, local environmental conditions to produce site-specific ecological patterns (e.g., Wernberg and Thomsen, 2005). Also, the ability to detect main effects of wave exposure over spatial interactions may depend on the measurement scale and definition of the wave exposure gradient (Lindegarth and Gamfeldt, 2005). Many of the mechanisms that could drive effects of wave exposure involve direct interaction between the understorey and the canopy (e.g., shading or abrasion). Effects of wave exposure may therefore be enhanced or negated, by concomitant changes in morphology of the canopy species between exposed an sheltered sites (Wernberg and Thomsen, 2005; Fowler-Walker et al., 2006).

In summary, we observed wave exposure and disturbances to have some effects on habitat structure and understorey assemblages, and these effects appeared to vary considerably in space over scales of 10 ms to kms. We were surprised that the benthic responses to such ubiquitous environmental differences and disturbance regimes could vary so widely within the narrow spatial context of some closely situated islands. It is possible that this variation may be explained by context-specific information (e.g. relative canopy composition). We suggest that the role of canopy composition in modifying ecological processes may deserve more attention. If habitats occur as mosaics, then a more explicit understanding of how composition mediates both ecological interactions and environmental conditions could help improve general models, including those about wave exposure and disturbances.

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