

Modification of the physical environment by an *Ecklonia radiata* (Laminariales) canopy and implications for associated foliose algae

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Abstract

Macroalgal canopies modify their surrounding environment and thereby influence the structure of associated algal assemblages. Canopies can modify many factors that can be hard to separate and, consequently, the importance of individual factors often remains unknown. Experiments were carried out to test the hypotheses that *Ecklonia radiata* canopies modify light, sediment cover and water motion, and that each of these physical factors separately influence the assemblage of associated foliose algae. We measured light, sediment cover and water motion across six naturally occurring *E. radiata* densities and found a reduction in light and sediment cover as kelp density increased. The outcome for water motion was inconclusive. We also manipulated each of these three factors, while controlling for the two others, to determine the separate effects of light, sediment cover and water motion on the assemblage of foliose algae. Reduction in light had a strong effect on the foliose assemblage, reducing species richness and biomass. Reduction in sediment cover and water motion did not cause separate effects at the level of the assemblage, but the biomass of individual species of foliose algae indicated both positive and negative effects. We conclude that *E. radiata* canopies at Marmion, Western Australia, modify at least two factors of their physical environment, light and sediment cover. However, only light is modified to an extent where it has effects at the assemblage-level because, in contrast to the effects of sediment cover and water motion, the direction of responses are consistent among individual species of algae.

Introduction

The presence of macroalgal canopies determines the distribution and abundance of associated organisms in many marine systems (Kennelly 1987, 1989; Edwards 1998; Kendrick et al. 1999, 2004; Melville and Connell 2001; Connell 2003; Toohey et al. 2004). Often, this is attributed to the influence these canopies have on physical factors such as light (Gerard 1984; Wood 1987; Kennelly 1989; Critchley et al. 1990), sediment deposition

(Eckman et al. 1989; Kennelly 1989), water motion (Jackson and Winant 1983; Eckman et al. 1989), scour (Velimirov and Griffiths 1979; Kennelly 1989) and temperature (Critchley et al. 1990). Most studies of how canopies modify the environment only test canopy presence vs. canopy absence. Yet, algal canopies occur in patches of varying density and cover (Schiel and Foster 1986; Kendrick et al. 1999) and this is reflected in the species richness and composition of the associated biota (Kendrick et al. 1999, 2004; Melville and

Connell 2001). Density-dependent habitat modification by algal canopies constitutes a causal link between the canopy and the understory community, but such effects remain largely unexplored and are addressed in this study.

Although subtidal algal canopies affect several different environmental factors relatively few studies (e.g. Kennelly 1989; Connell 2003; Toohey et al. 2004) have attempted to separate these canopy effects into their different components and, in many cases, the specific mechanisms underlying the influence of canopies on the structure of associated communities remain unknown or unclear (Jones et al. 1994; Bertness et al. 1999). Identifying the effects of individual factors is difficult in canopy-dominated habitats because many of the environmental factors that are modified covary (Dayton 1985) and, therefore, careful experimentation is needed to control for and separate these effects. Nonetheless, understanding how communities and their components are affected by different environmental conditions is essential for our ability to predict responses to changes in the physical environment and macroalgal canopy cover (Keddy 1992), for example caused by human activities (Vogt and Schramm 1991; Benedetti-Cecchi et al. 2001).

In this study we focus on light, sediment cover and water motion because these three factors are affected by macroalgal canopies and have been identified as important to the organization of marine communities (light: Kennelly 1989; Irving and Connell 2002; Toohey et al. 2004; sediments: Kendrick 1991; Airoidi and Cinelli 1997; Eriksson et al. 2002; water motion: Phillips et al. 1997; Leliaert et al. 2000). Moreover, these three physical factors are particularly hard to separate as moving water resuspends (Komar and Miller 1973) and redistributes (Daly and Mathieson 1977) sediments. Suspended sediment particles attenuate light and reduce bottom irradiance (Dean 1985), and they also abrade and smother benthic organisms (Daly and Mathieson 1977; D'Antonio 1986; Fabricius and Wolanski 2000). This inter-dependence can confound experimental tests of canopy effects such as when Kennelly (1989) observed sediment accumulation under roof structures deployed to mimic light levels below *Ecklonia radiata* canopies.

We tested the hypotheses that (1) *E. radiata* canopies modify light, sediment cover and water

motion according to their density, and (2) that each of these physical factors influence the foliose algae associated with the canopy habitat. We addressed these hypotheses by conducting a mensurative experiment to compare light, sediment cover and water motion among different naturally occurring kelp densities, and a series of manipulative experiments to test the effect of each of these three factors, while controlling for the two others, on the foliose algae associated with kelp beds.

Materials and methods

Study site

The study was done at Marmion which is located north of Perth, Western Australia. Marmion has several parallel limestone reefs (Searle and Semeniuk 1985) that host a diverse algal assemblage dominated by a prostrate canopy of the small kelp *E. radiata* (C. Ag.) J. Agardh (Kendrick et al. 1999; Wernberg et al. 2003). These reefs are separated by areas of coarse quartz and calcium carbonate sand which is resuspended and deposited on the reef surfaces intermittently. The hydrodynamic regime in the region is dominated by wind and swell generated waves (Searle and Semeniuk 1985). Experiments were done close to Horseshoe Reef (31°50.230' S 115°42.850' E) on a moderately exposed (cf. wave energy at intermediate reef line in Phillips et al. 1997), low relief (< 2 m) reef flat where the general canopy cover of *E. radiata* was estimated to be 70–90% of the substratum. To further characterize the study site, depth and density of grown *E. radiata* sporophytes (stage 3 *sensu* Kirkman 1981) was determined within 28 randomly positioned 0.25-m² quadrats (cf. the plots described later) and found to be 7.1 m ± 0.2 SE and 10.8 sporophytes m⁻² ± 1.4 SE, respectively.

There were three components to our study. First, we tested the effect of naturally occurring kelp densities on sub-canopy levels of light, sediment cover and water motion. Second, we tested the effect of each of these physical factors on foliose algae and, third, we tested the efficiency of our experimental manipulations. Because the outcome of the test for efficiency of our manipulations is fundamental to understanding the combinations of treatments used to test effects of the physical factors on foliose algae, we present the results in

the methods section while describing the structure and function of individual treatments (cf. Treatments and *a priori* planned contrasts).

Effect of kelp density on the physical environment

Light, sediment cover and water motion were measured within 0.25-m² quadrats across six naturally occurring kelp densities of 0, 1, 2, 3, 4 and > 5 grown sporophytes 0.25 m⁻². Four replicates of each kelp density was sampled independently for each factor (i.e. a total of 72 quadrats were sampled).

Light, measured as down-welling bottom irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$) over a 100 s integration time, was quantified with a quantum photometer (Li-Cor Inc., model L1-188B) in the centre of the 0.25-m² quadrat. Light measurements were done just after noon on a calm day with clear skies in December 2001. Replicates from all kelp densities were sampled in random order to avoid any bias caused by the position of the sun.

Sediment cover (g DW 0.0625 m⁻²) was measured within a 25 cm \times 25 cm (0.0625 m²) quadrat in the centre of the 0.25-m² quadrat. Unconsolidated sediments were collected (suction time = 30 s) in 200- μm mesh bags with a venturi suction sampler. The samples were rinsed in fresh water, biota removed and sediments filtered onto coffee filters (maximum pore size 100 μm) which were then dried at 75 °C until constant weight, and weighed.

Water motion (g DW lost day⁻¹) was measured with clod cards made of casting plaster (CaSO₄) with latex paint added to decrease the dissolution rate. Two clod cards (18.0 g DW \pm 0.2 SE) were attached to a brick covered with a 1 cm \times 1 cm wire mesh cage to protect against abrasion from algal fronds. Each brick was placed in the centre of the 0.25-m² quadrat and left for four and a half days. The clod cards were then collected, dried at 75 °C until constant weight and re-weighed. Dissolution rates (g DW lost day⁻¹) of individual clod cards were averaged for each brick.

Effects of physical environment on foliose macroalgae

Three experiments were carried out that manipulated either light, sediment cover or water motion

while maintaining each of the other two factors constant. The experiments were designed as *a priori* planned contrasts among appropriate treatment combinations (see 'Treatments and *a priori* planned contrasts' below and Figure 1). We chose this approach to reduce overall numbers of treatments and replicates to a manageable amount, and to avoid treatments that we were not confident about constructing *in situ*.

Twenty-eight 1.5 m \times 1.5 m plots were established and randomly assigned to one of seven treatments, with four replicates per treatment. Plots were separated by at least 2 m. There were no differences in depth (one-way ANOVA; $F_{(6,21)} = 0.64$; $p = 0.70$) or pre-manipulation densities of *E. radiata* (one-way ANOVA; $F_{(6,21)} = 0.67$; $p = 0.68$) among treatments. Prior to implementing treatments all grown sporophytes were removed from the experimental plots (except the 'kelp treatment') by cutting the stipes immediately above the holdfast.

The experiments commenced late November 2000 (early austral summer) and ran for five

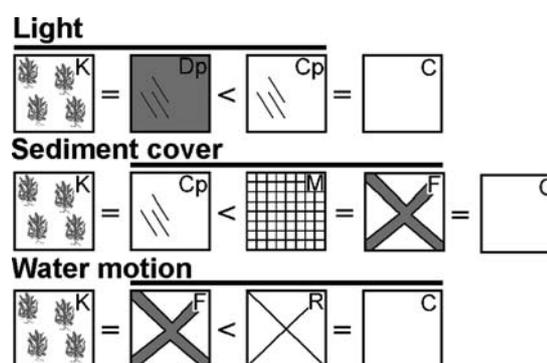


Figure 1. Schematic of the experimental treatments and their combinations used to obtain separate tests of the effect of light, sediment cover and water motion on foliose algae associated with *Ecklonia radiata* canopies. 'K' (kelp treatment): kelp canopy left untouched. In all other treatments the kelp canopy was first removed by cutting the stipes immediately above the holdfast. 'C' (clear treatment): kelp canopy removed. 'Cp' (clear PVC treatment) and 'Dp' (dark PVC treatment): plot covered by a sheet of clear or black PVC. 'M' (mesh treatment): plot covered by a sheet of 5 cm \times 5 cm plastic mesh. 'F' (fence treatment): a 20 cm high hessian fence suspended ca. 10 cm above the plot across both diagonals. 'R' (rope treatment): a 20 mm rope suspended ca. 10 cm above the plot across both diagonals. To ensure that the physical environment tested was equivalent to that either under dense canopy cover or in open areas, both 'K' and 'C' treatments were included in the test of efficiency of treatments. Bold lines indicate treatments combined to test effects on foliose algae.

months after which the effects on foliose algae were assessed. During this period treatments were maintained at least fortnightly. Upon closing the experiments all foliose macroalgae within the centre 0.25-m² of each plot were harvested by hand-picking aided by a paint scraper. Samples were stored frozen (-18 °C) until processed. All macroalgae were identified to lowest possible taxonomic unit and then dried at 60 °C until constant weight before weighing.

Efficiency of experimental manipulations

Pilot studies had indicated the efficiency of each treatment type, but to minimize disturbance to the algae in the experimental plots, formal tests of how well our treatments manipulated the physical environment were only conducted after the end of the experiments testing effects on foliose algae. All treatments were reset in three replicates. Light, sediment cover and water motion were measured in the centre of each plot using the previously described methods. To ensure that the levels of treatment manipulations mimicked the two extreme situations in the kelp bed, dense canopy and open patches, both canopy and open plots were included in the planned contrasts when testing the environmental conditions (Figure 1).

Treatments and a priori planned contrasts

The effect of light on foliose algae was tested by comparing plots of intact kelp canopy with cleared plots covered with sheets of dark or clear PVC (Figure 1). The kelp canopy and the dark PVC had similar low light levels ($K = Dp$; $F_{(1,8)} =$

0.001, $p=0.99$), whereas the clear PVC allowed full light penetration ($Cp = C$; $F_{(1,8)} = 0.05$, $p=0.83$) to provide significantly more light ($K + Dp < Cp + C$; $F_{(1,8)} = 213$, $p < 0.001$; Table 1). All treatments in this combination had roof structures and thus similar effects ($K = Dp = Cp$) on sediment cover ($F_{(2,6)} = 4.8$, $p=0.06$) and presumably water motion (could not be tested due to clod cards in the kelp canopy treatment being damaged by a storm). The presence of kelp fronds in one of the low-light treatments was assumed to be unimportant as scour from *E. radiata* fronds do not affect foliose algae in the understorey (Kennelly 1989; Toohey et al. 2004).

The effect of sediment cover was tested by comparing the clear PVC treatments with cleared plots which were either covered by sheets of 5 cm × 5 cm plastic mesh or had 20 cm high hessian fences suspended 10 cm above the bottom across both diagonals (Figure 1). As in open plots, sediments could settle unrestricted in both mesh and fence treatments ($C = M = F$; $F_{(1,10)} = 2.85$, $p=0.12$), whereas the PVC, like the kelp canopy ($K = Cp$; $F_{(1,10)} = 0.06$, $p=0.81$), acted as a barrier resulting in lower sediment cover under the clear PVC than under the mesh and in the fence treatments ($K + Cp < M + F + C$; $F_{(1,10)} = 21.6$, $p=0.001$; Table 1). All treatments in this combination had light levels similar to gaps in the canopy ($Cp = M = F$; $F_{(2,6)} = 0.35$, $p=0.72$) and either roof or vertical structure to dissipate water motion as under a kelp canopy ($Cp = M = F$; $F_{(2,6)} = 0.02$, $p=0.82$). Fence treatments acted as control for the effect of roof structures on light ($M = F$; $F_{(1,10)} = 0.28$, $p=0.61$).

The effect of water motion was tested by comparing the fence plots with similar plots which had ropes suspended across both diagonals, and the open plot treatment (Figure 1). Water moved

Table 1. Mean levels (standard error, $n=3$) of physical factors in each treatment.

Physical factors	Kelp	Dark PVC	Clear PVC	Mesh	Fence	Rope	Clear
Light ($\mu E m^{-2} s^{-1}$)	1.3 (0.5)	0.7 (0.2)	616 (64)	547 (40)	690 (150)	640 (10)	629 (56)
Sediment cover (g DW 0.0625 m ⁻²)	23.6 (2.1)	29.4 (3.2)	37.1 (3.7)	152.3 (43.6)	180.9 (50.4)	217.3 (60.3)	245.8 (53.7)
Water motion (g DW lost day ⁻¹)	nd. ^a	1.31 ^b (0.30)	1.31 ^b (0.30)	1.42 (0.41)	1.61 (0.27)	2.96 (0.14)	2.43 (0.16)

^aNo data because of damaged treatments.

^bOnly tested for 'PVC covered treatments' because of damaged treatments; assumed to be identical between dark and clear PVC.

unrestricted through open and rope treatments ($C = R$; $F_{(1,6)} = 3.7$, $p = 0.10$), whereas water motion was lower in the fence treatments ($F < R = C$, $F_{(1,6)} = 20.7$, $p = 0.004$; Table 1) because the fences dissipated flow. All these treatments were without roof structures to interfere with light ($F = R = C$; LOG_{10} -transformed data, $F_{(2,6)} = 0.4$, $p = 0.96$) and settling sediments ($F_{(2,6)} = 0.35$, $p = 0.72$). The rope moved in the surge as the fence and acted as a control for possible scouring effects.

Statistical analyses

The effect of kelp density on the physical environment was tested with one-way ANOVA followed by SNK tests for each dependent variable. For sediment cover and water motion, only three replicates were sampled for some kelp densities (1 and > 5 , and 3 sporophytes 0.25 m^{-2} , respectively) and the average of the three replicates was added as a fourth pseudo-sample to balance the design. Degrees of freedom for the $\text{MS}_{\text{residual}}$ were adjusted accordingly.

The treatment effects and efficiencies (Figure 1, Table 2) were tested with one-way ANOVA followed by planned contrasts when H_0 was rejected ($p < 0.05$). Multivariate analyses of species composition were performed in PRIMER. A

Bray–Curtis similarity matrix was calculated from square root-transformed data on species biomass. The global H_0 of no differences in assemblage structure among the *a priori* defined treatment groups was tested with one-way analysis of similarities followed by pair-wise comparisons, and then graphed in a non-metric MDS plot.

All data were checked for homogeneity of variances using Cochran's *C*-test and transformed when $p < 0.05$.

Results

Effects of kelp canopy on the physical environment

Kelp canopies had a significant effect on light ($F_{(5,18)} = 62$; $p < 0.001$) and sediment cover (LOG_{10} -transformed data; $F_{(5,16)} = 6.0$; $p = 0.003$) but not on water motion ($F_{(5,17)} = 1.48$; $p = 0.25$). SNK-tests ($p < 0.05$) were consistent with a progressive reduction in light and sediment cover with increasing kelp density (Figure 2).

Light levels were slightly less than $800 \mu\text{E m}^{-2} \text{ s}^{-1}$ in open patches (0 kelps 0.25 m^{-2}) and declined to just over $10 \mu\text{E m}^{-2} \text{ s}^{-1}$ in dense kelp patches (> 5 kelps 0.25 m^{-2}). There was a significant

Table 2. Results from one-way ANOVA and planned contrasts testing the effect of treatments on the macroalgal assemblage.

Physical factors	DF	Species richness			Biomass		
		MS	F	P	MS	F	P
<i>Light (K = Dp < Cp)</i>							
Cochran's <i>C</i>		$C = 0.68$; $p < 0.01$			$C = 0.75$; $p < 0.01$		
Among treatments	2	318.3	45.8	<0.001	1724	33.8	<0.001
K vs. Dp	1	6.1	0.9	0.38	53.4	1.1	0.35
K + Dp vs. Cp	1	630.4	90.8	<0.001	3395	66.6	<0.001
Residual	9	0.9			51.0		
Total	11						
<i>Sediment cover (Cp < M = F)</i>							
Cochran's <i>C</i> -test		$C = 0.49$; $p < 0.01$			$C = 0.37$; $p < 0.01$		
Among treatments	2	3.0	0.2	0.81	307.6	2.8	0.11
Residual	9	13.8			108.7		
Total	11						
<i>Water motion (F < R = C)</i>							
Cochran's <i>C</i> -test		$C = 0.58$; $p < 0.01$			$C = 0.77$; $p < 0.01$		
Among treatments	2	101.1	2.3	0.16	54.1	0.3	0.75
Residual	9	44.7			183.4		
Total	11						

Treatment abbreviations are as in Figure 1.

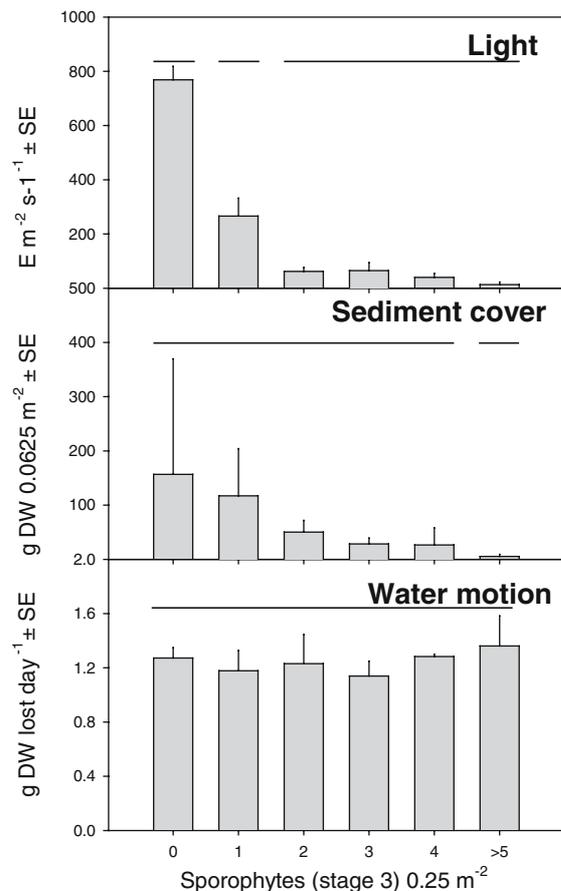


Figure 2. Light, sediment cover, and water motion under different naturally occurring kelp canopy densities. Lines indicate groups that are not significantly different (SNK tests, $p < 0.05$).

decrease in light levels from 0 to 2 kelps 0.25 m^{-2} after which increasing canopy density had no additional effect on sub-canopy light availability. The sediment cover of open patches was slightly less than $160 \text{ g DW } 0.0625 \text{ m}^{-2}$ and declined gradually to just over $5 \text{ g DW } 0.0625 \text{ m}^{-2}$ in dense kelp patches. Only the densest patches were significantly different from open and low density patches, although a clear decreasing trend was evident across all canopy density categories. The clod cards deployed to measure water motion had plaster dissolution rates of just over $1.2 \text{ g DW lost day}^{-1}$ regardless of kelp density. However, obvious scars from frond abrasion indicated that the cages under the canopy did not protect the plaster blocks adequately, and the cages deployed in open patches quickly became fouled by drifting filamentous algae which, by the end of the

deployment, completely covered the cages restricting water flow over the clod cards.

Effects of the physical environment on foliose algae

For light to have an effect it was hypothesized that kelp canopy = dark PVC \neq clear PVC. This hypothesis was supported for all of the measured assemblage characteristics (Tables 2 and 3). Kelp canopy and dark PVC treatments had less than 10 macroalgal species 0.25 m^{-2} which was significantly less than the over 20 species 0.25 m^{-2} in the clear PVC treatment (Figure 3). The effect of light on assemblage biomass was even more profound as the low light treatments had less than $15 \text{ g DW } 0.25 \text{ m}^{-2}$ and the high light treatment almost $45 \text{ g DW } 0.25 \text{ m}^{-2}$.

For sediment cover and water motion to have an effect it was hypothesized that clear PVC \neq mesh = open plot and fence \neq rope = open plot, respectively. None of these hypotheses could be supported as neither species richness or biomass of the assemblage were affected by the manipulations of sediment cover and water motion (Tables 2 and 3). Species richness for all these treatments were around 20 species 0.25 m^{-2} and they all had a biomass of approximately $45 \text{ g DW } 0.25 \text{ m}^{-2}$ (Figure 3).

In the tests of species composition, the low light treatments (kelp and dark PVC) formed a group distinctly separated from the rest of the treatments (Table 3, Figure 4). Algal assemblages in treatments manipulating sediment cover and water motion did not separate into distinct groups.

Individual species were affected differently by the various treatments (Figure 5). Only four species, *Pterocladia lucida*, *Rhodymenia sonderi*, juvenile *E. radiata* and *Heterodoxia denticulata* were found in all treatments. All species, except *P. lucida* which had higher biomass, had lower or no biomass under low light compared to high light conditions. Seven species indicated effects of sediment cover: *R. sonderi*, *E. radiata* juveniles, *H. denticulata*, *Ulva rigida*, *Chauvinella coriifolia*, *Dictyomenia sonderi* and *Sargassum* subg. *Arthrophyucus*. The direction of their responses were however not the same. *E. radiata* juveniles, *H. denticulata*, *U. rigida*, *C. coriifolia* and *Sargassum* subg. *Arthrophyucus* had higher biomass, whereas *R. sonderi* and *D. sonderi* had lower biomass under low sediment cover. Four species

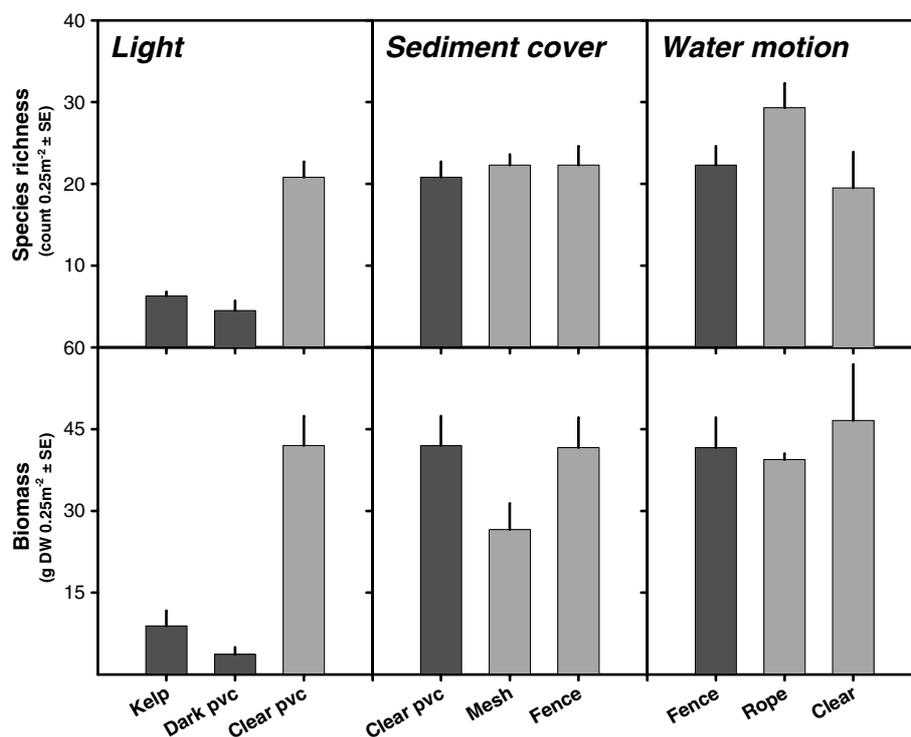


Figure 3. Species richness and biomass in the treatments for each set of *a priori* contrasts testing the effect of light, sediment cover and water motion on algal assemblages. Dark and light bars indicate canopy and gap conditions, respectively.

indicated effects of water motion: *P. lucida*, *Jeanerettia pedicillata*, *R. sonderi* and *Sargassum* subg. *Arthrophycus*. *P. lucida* and *R. sonderi* had higher biomass, whereas *J. pedicillata* and *Sargassum* subg. *Arthrophycus* had lower biomass under reduced levels of water motion (Figure 5).

Table 3. Results of pair-wise comparisons among treatments following ANOSIM, testing the effect of treatments on algal assemblage structure.

	<i>R</i>	<i>p</i>	Interpretation
Light			
K vs. Dp	0.031	0.429	
K vs. Cp	1.000	0.003	
Dp vs. Cp	0.969	0.003	K = Dp ≠ Cp
Sediment cover			
F vs. M	0.146	0.343	
F vs. Cp	0.375	0.371	
M vs. Cp	0.198	0.171	F = M = Cp
Water motion			
C vs. R	-0.240	0.886	
C vs. F	-0.052	0.600	
R vs. F	-0.094	0.743	C = R = F

Treatment abbreviations are as in Figure 1.

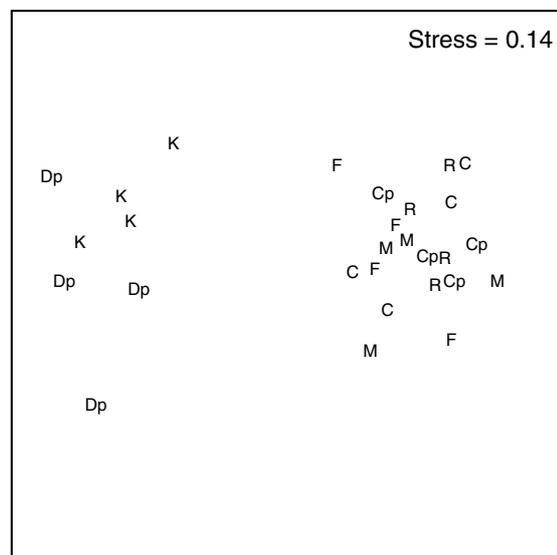


Figure 4. nMDS plot of similarity in assemblage structure among treatments calculated from square root-transformed biomass data of each species per 0.25 m². Treatment abbreviations are as in Figure 1.

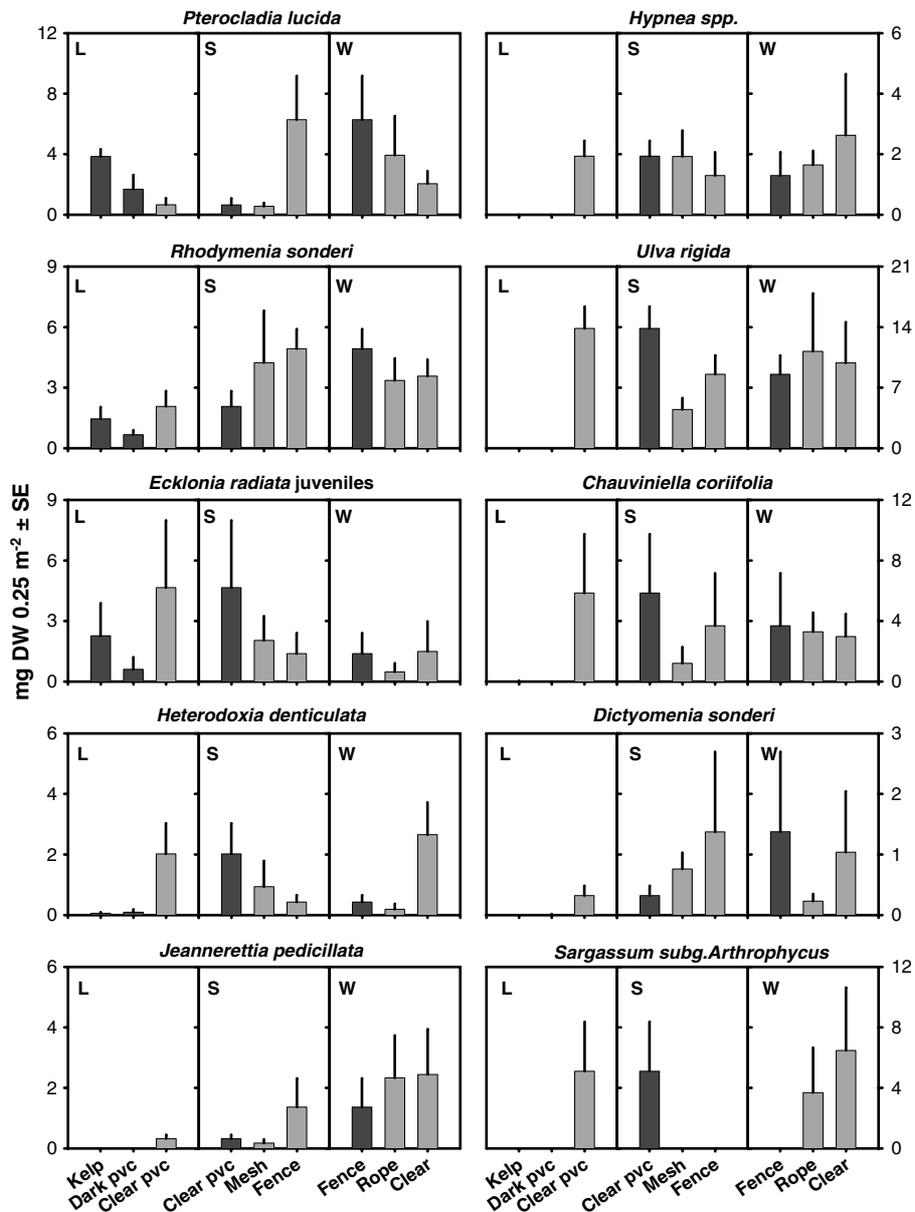


Figure 5. Biomass in the treatments for each set of *a priori* contrasts testing the effect of light, sediment cover and water motion on selected foliose algal species. Note the different scaling of axes. L: treatments testing the effect of light; S: treatments testing the effect of sediment cover; W: treatments testing the effect of water motion. Dark and light bars indicate canopy and gap conditions, respectively.

Discussion

Canopy effects on light and associated effects on foliose algae

There was a steep decline in understorey light levels as the density of *E. radiata* canopies increased. Macroalgal canopies are physical barriers to light

and previous studies have also found that both floating surface canopies (Gerard 1984; Critchley et al. 1990) and subsurface canopies (Wood 1987; Kennelly 1989) are capable of reducing sub-canopy light to a few percent of above-canopy levels. Gerard (1984) found an exponentially declining relationship between canopy density and light penetration through the surface canopy of a *Macrocystis pyrifera*

forest. Our results for the prostrate canopy of *E. radiata* at Marmion are consistent with her findings and suggest that even a sparse canopy of 1–2 sporophytes 0.25 m^{-2} can reduce light penetration to levels that potentially affect algae in the understory ($< \sim 200 \mu\text{E m}^{-2} \text{ s}^{-1}$, Lüning 1981). We measured sub-canopy light on a relatively calm day and using a relatively long integration time. It is possible, therefore, that more sub-canopy light is available on days with higher water motion where more light flecks penetrate through the moving canopy (Gerard 1984). On these days, however, water motion is also likely to increase turbidity and thus reduce overall light penetration through the water (Dean 1985). Even if our results underestimate the sub-canopy light levels in the presence of more light flecks, there is no reason to believe that this will offset the density-dependent effect of *E. radiata* canopies on sub-canopy light levels.

Low light levels significantly reduced species richness and biomass of the assemblage of associated foliose algae. This was because the effect of low light levels was consistent across the majority of species. Macroalgae differ in their ability to utilize ambient light by the composition and abundance of their light-harvesting pigments (Lobban and Harrison 1994). If light levels are below a critical level where production is less than combined loss processes such as respiration, grazing and tattering, macroalgae cannot persist. This critical level is determined in part by physiological and anatomical differences among species (King and Schramm 1976; Markager and Sand-Jensen 1992) and in part by photo-acclimation within species (King and Schramm 1976; Henley and Ramus 1989). The lower species richness and biomass in the low light treatments suggest that light levels beneath the kelp canopy are lower than or close to the compensation points of most species in the foliose assemblage. Only *P. lucida* had a higher biomass in low compared to high light conditions. However, it cannot be inferred from this study whether this positive response is a physiological effect of low light *per se* or an effect of competitive release.

The responses of individual species to the light treatments indicated that there are three core members of the foliose algal assemblage associated with kelp beds at Marmion: *P. lucida*, *R. sonderi* and *E. radiata* juveniles. When light levels are low, such as beneath the canopy, the assemblage consists

almost entirely of these three species. In the gaps in the canopy, where photon flux is relatively high, other foliose species are added to the assemblage (Kendrick et al. 1999, 2004). The presence of *P. lucida*, *R. sonderi* and *E. radiata* juveniles regardless of irradiance levels suggest that they have wider photo-acclimative ranges than other macroalgae in the assemblage (see also Toohey et al. 2004).

Canopy effects on sediment cover and associated effects on foliose algae

The sediment cover was reduced under high *E. radiata* canopy densities. This effect is likely linked to the low abundance of foliose vegetation that trap sediment, and the sweeping by kelp fronds (Kennelly 1989) which increases the mobility of sediments. Once re-suspended, the sediment particles may 'bounce' off the canopy (Eckman et al. 1989) and become deposited in areas with sparse or no canopy (Kennelly 1989) where they are trapped and retained in the turf and among the foliose algae (Stewart 1983; Kendrick 1991; Airoidi et al. 1995).

Several studies have demonstrated that sediment can affect macroalgal communities (Daly and Mathieson 1977; Kendrick 1991; Airoidi and Cinnelli 1997; Connell 2003). However, in this experiment at Marmion, *E. radiata* canopies did not modify sediment cover sufficiently to have separate assemblage-wide effects on the associated foliose algae. Our tests for effects of sediment cover were conducted under high light conditions and it cannot be ruled out that sediments will have stronger effects under low light conditions (Irving and Connell 2002). In relation to effects of canopies however, only the scenario tested in this study is realistic as canopies reduce both light and sediment cover. Although there were no effects at the level of the assemblage, the biomass of individual species responded both positively (e.g. *D. sonderi* and *R. sonderi*) and negatively (e.g. *E. radiata* juveniles and *Sargassum* subg. *Arthrophyucus*) to the manipulations of sediment cover. These species-specific differences may reflect morphological and physiological adaptations causing differences in the sensitivity to particulate abrasion and burial (Daly and Mathieson 1977; D'Antonio 1986). In particular, the apparent positive effects of sediments on *D. sonderi* and *R. sonderi* correspond to similar effects reported for other red algae

(reviewed by Airoidi 2003). Again, however, it cannot be inferred from this study whether this is an effect of competitive release from more sediment-sensitive species or a positive physiological response by the species themselves. Recruitment and colonization stages appear to be particularly sensitive to variations in the depositional environment (Kendrick 1991; Airoidi and Cinelli 1997; Isaeus et al. 2004). This is probably because sediments interfere with propagule attachment and survival (Deviny and Volse 1978; Berger et al. 2003; Isaeus et al. 2004).

Canopy effects on water motion and associated effects on foliose algae

We were unable to demonstrate an effect of *E. radiata* canopy on water motion. One would expect a negative effect of canopies on water motion because of the obstruction by vertical canopy structures. This has been demonstrated for stipitate (Eckman et al. 1989) and surface kelp canopies (Jackson and Winant 1983) as well as for seagrasses (Ackerman and Okubo 1993; Worcester 1995).

We found no assemblage-wide effects of water motion on foliose algae but as for sediment cover, responses of individual species to reduction in flow indicated both positive (e.g. *R. sonderi*) and negative (e.g. *Sargassum* subg. *Arthrophyucus*) effects.

Water motion is correlated to almost every possible physical factor or process in water (see review by Hurd 2000). It is therefore particularly likely that water motion will interact with the effects of other environmental factors, including light and sediment cover. This study did not test for such interactions. However, as a consequence of mechanical drag, water motion may also have direct effects separate of all other factors (Denny 1995). Hence, species-specific differences in responses to our treatments manipulating water motion could be due to differences in biomechanical properties which affect the susceptibility to dislodgment and tattering (Dudgeon and Johnson 1992; Shaugnessy et al. 1996).

Assemblages vs. species

The apparent effect of macroalgal canopies on associated foliose algae is a combination of positive

and negative effects of individual factors on individual species in the assemblage. When assemblages are characterized by univariate measures such as total biomass or species richness, these species-specific effects combine to produce effects at the assemblage level only if they are consistent across the dominant species, such as it was the case for the effect of light. If responses of individual species are weak or have opposite directions they will sum up to have no effects at the assemblage level, as it was the case with sediment cover and water motion. Differences in responses of individual species to changes in the physical environment (see also Kennelly 1987; Kennelly and Underwood 1993) highlight a significant problem of only assessing univariate summary statistics (e.g. total biomass, cover or species richness) for subtidal algal assemblages. For example, despite substantial changes in the identity of species, Santelices and Ojeda (1984) found no changes to species richness of foliose algae in the understory, following removal of a *Macrosystis pyrifera* canopy in Chile. In particular, the opposite responses of morphologically similar species (e.g. *P. lucida* and *R. sonderi* in this study) emphasize the difficulties of extrapolating between organizational levels without loss of important ecological information (Phillips et al. 1997). Because there are significant physiological (Dudgeon et al. 1995) and biomechanical (Shaugnessy et al. 1996) differences between species with similar morphologies, caution must be taken if lumping species into coarse form-functional groups, particularly when groups are based on assumptions of similarity in function solely from superficial characters.

Conclusions

Canopies of *E. radiata* have a density-dependent effect on light and sediment cover. Of the physical factors modified by the kelp canopy, only light was found to have a separate assemblage-wide effect on foliose algae, reducing total biomass and species richness. Canopy-modification of sediment cover and water motion had no assemblage-wide effects but individual species responded both positively and negatively. Our study emphasizes that although canopies modify several environmental conditions which may co-vary, each of the individual factors may have separate effects on foliose

algae. Field experiments that partition components of effects of subtidal canopies on their surroundings are still needed in order to understand how these structurally important organisms influence community structure. In particular, experiments that explicitly include water motion in a manipulative context are currently lacking. Moreover, our study highlights that even relatively similar species may be oppositely affected by these canopy-modified environments and that only assessing effects on higher organizational levels therefore may be associated with significant loss of ecological information.

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