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RESEARCH ARTICLE

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The effects of light and thallus scour from *Ecklonia radiata* canopy on an associated foliose algal assemblage: the importance of photoacclimation

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Abstract Kelp canopies have long been recognised for their influence on the structure of algal assemblages on sublittoral reefs. In Marmion Lagoon, Western Australia, we investigated how a canopy of the small kelp *Ecklonia radiata* affected the associated foliose algal assemblage and what potential mechanisms were responsible for the effects we observed. Light levels and physical abrasion (thallus scour) by an *E. radiata* canopy were manipulated in an orthogonal fixed-factor experiment that revealed that changes in light, but not thallus scour, had a significant effect on the composition of the algal assemblage. Reduced light levels were associated with a decrease in the Shannon-Wiener diversity index and an increased dominance of the foliose algae *Pterocladia lucida* and *Rhodymenia sonderi*. Photobiological investigations of three foliose species, *P. lucida*, *R. sonderi* and *Chauviniella coriifolia* indicated that they were able to photoacclimate to low light levels by increasing thallus absorption by up to 11%. Photoacclimation was also evident by an increase in the maximum rate of electron transport under low-light conditions. We conclude that the *E. radiata* canopy in Marmion Lagoon structures the foliose algal assemblage through the modification of the light environment and that this effect may be mediated by differences in the ability of different species of foliose algae to photoacclimate.

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Introduction

Many algal assemblages are dominated by a canopy-forming kelp or fucalean species that exerts an influence on the composition of the rest of the assemblage. The compositions of many algal assemblages have been found to differ under canopies compared to open patches (Dayton et al 1984, 1992; Kennelly 1987a, b; Kendrick et al. 1999, 2003; Melville and Connell 2001; Connell 2003a). The removal of the dominant canopy-forming species, by storms for example (May and Larkum 1981; Kennelly 1987a), results in large and generally positive changes in the biomass, species richness and species composition of algal assemblages (Pearse and Hines 1979; Kennelly 1987a, b; Kendrick et al. 2003). The abundances of foliose and coralline algal species have been found to be lower under canopies than in areas without a canopy (Rapp de Eston and Bussab 1990; Kendrick et al. 1999, 2003; Melville and Connell 2001; Connell 2003a). Kendrick et al. (1999) documented that the influence of an *Ecklonia radiata* canopy was species-specific with the foliose red alga *Dictyomenia sonderi* displaying a significant reduction in abundance under the canopy while *Pterocladia lucida* did not.

Kelp canopies have been shown to modify several aspects of the physical environment, including reducing sub-canopy light levels (Wood 1987; Kennelly 1989; Wernberg-Moller 2002). It has been shown that in many kelp forests, the effect of the canopy on the understorey can be explained by modification of the light environment. Canopy shading has been demonstrated in *Macrocystis pyrifera* kelp forests of California and in the *Ecklonia* kelp beds of Australia (Cowen et al. 1982; Reed and Foster 1984; Kennelly 1989; Wernberg-Moller

2002). The mechanism underlying the influence on foliose algae of a reduction in light has been less studied. Some foliose species are found to dominate under canopies whereas others are restricted to high-light gaps in the canopy. This paper addresses individual species' responses to different light environments.

In *Macrocystis* forests the evidence for canopy shading is extensive, and assemblage changes can be clearly attributed to shading by a canopy that floats at the water's surface (Kennelly 1994). However, as an *E. radiata* canopy lies relatively close to the substratum, it not only reduces sub-canopy light levels but also scours the substratum (Fletcher and Day 1983; Kennelly 1989; Connell 2003b), and hence some of the effect of an *Ecklonia* canopy on the understorey assemblage could also be explained by thallus scour rather than canopy shading alone.

The only study to look simultaneously at the effect of *E. radiata* canopy shading and thallus scour on the understorey algal assemblage was by Kennelly (1989). He carried out two individual experiments, one on each factor, and concluded that thallus scour had no significant effects on the assemblage and that reduced light alone could explain the canopy's influence on the understorey. However, Kennelly's study was conducted in a sheltered embayment (Sydney Harbour, New South Wales), where exposure to oceanic swells was relatively low. Thallus scour may prove to have an equal or greater influence as compared with canopy shading in more exposed locations where large swell frequently creates intense scouring of the substratum. Furthermore, as other factors, such as sediments, have been shown to have an interactive effect with light on algal assemblages (Connell 2003a), thallus scour may also interact with canopy shading in its effect on the foliose algal assemblage. In this study we have conducted an experiment which looks at both individual and interactive effects of light and thallus scour on the foliose algal assemblage in an exposed location.

From previous research, it was already known that a proportion of the effect of an *E. radiata* canopy could be explained by canopy shading (Kirkman 1985; Kennelly 1989; Wernberg-Moller 2002; Irving and Connell 2003), and hence the second half of our research attempted to explain the effect of canopy shading on a physiological level. Given that the effects of a canopy on foliose algae are species-specific (Kendrick et al. 1999), some species may be more adapted to living in low-light environments underneath the canopy than others. However, as the distribution of these low-light adapted species is not confined to the area underneath the canopy but extends metres away outside the canopy in high-light conditions, adaptation to low light may occur phenotypically in these species.

Phenotypic adaptation of photobiology is known as photoacclimation (Gantt 1990) and is characterised by a change in the pigmentation, light-use efficiency and maximum photosynthetic rate of an alga. Changes in pigmentation are associated with changes in the amount of light that thalli can absorb (Markager and Sand-Jensen 1994). Photoacclimation to low-light conditions is typically an increase in pigmentation and light-use efficiency and a decrease in the maximum photosynthetic rate (Ramus et al. 1976, 1977). These changes increase the amount of light that can be used in photosynthesis and hence increase the utilisation of a limited resource (Gantt 1990). We hypothesised that the response of individual species to low light levels created by the canopy is related to their photoacclimative abilities.

Our aim in this research was to determine the mechanisms underlying the effects of an *E. radiata* canopy on the associated foliose algal assemblage. In this study we tested whether light and thallus scour had independent or interactive effects on the foliose algal assemblage in a wave-exposed location. This led us to investigate differences in photoacclimative abilities between foliose algal species, and whether they could explain how a reduction in the light levels resulted in changes in the composition of the foliose algal assemblage.

Materials and methods

Study site

Our research focused on the foliose members of the algal assemblage and was divided into two parts; a manipulative experiment and photobiological investigations. All fieldwork was carried out by SCUBA in Marmion Lagoon (31° 50.237′ S, 115° 42.876′ E), 20 km north of Perth, Western Australia. Marmion Lagoon is a semi-enclosed embayment and has a foliose algal assemblage composed of a canopy of the small prostrate kelp *E. radiata* (C. Ag.) J. Agardh, and a suite of associated Rhodophyta (Phillips et al. 1997). Marmion Lagoon has a series of three reef lines running parallel to the shore and is frequently exposed to large ocean swell (Searle and Semeniuk 1985). Further descriptions of Marmion Lagoon can found in Kirkman (1981, 1984), Phillips et al. (1997) and Kendrick et al. (1999).

Experimental manipulations of light and thallus scour

Experimental design

Experimental manipulations were conducted between 7 January 2002 and 1 March 2002 to determine the independent and interactive effects of light and thallus scour on the foliose algal assemblage. Manipulations were conducted on a low-relief limestone reef in the second reef line with a medium level of wave/swell exposure (Phillips et al. 1997), with a typical swell height ranging from 1 to 3 m.

The experiment consisted of two levels for each factor, with high and low light levels being orthogonally crossed with high and low levels of thallus scour, to give a total of four experimental treatment combinations. Each treatment combination had four replicates. Fifty-four days after the application of treatments, the foliose algal assemblage was sampled to determine if the different combinations of light and thallus scour had resulted in shifts in the composition of the assemblage.

Pre-manipulation conditions

Sixteen plots, 1 m^2 in size, at a depth of 6.1 ± 0.5 m (mean ± SE, $n = 16$) were created by the removal of the *E. radiata* canopy by cutting the stipe close to the holdfast. To confirm that plots did not significantly differ at the start of the experiment, initial kelp density and foliose algal assemblage composition was quantified. Kelp density was determined by counting all the adult sporophytes (defined as stage 3 by Kirkman 1981) as they were removed from the plots. Assemblage composition was determined by visual qualitative estimates of the percentage cover of each algal species within the central 0.25 m^2 of the plots.

Plots did not significantly differ at the start of the experiment in terms of pre-manipulation kelp densities or foliose algal assemblage composition. For kelp density, results for one-way analysis of variance (ANOVA) were as follows: Cochran's $C = 0.482$, $C_{crit(0.05,4,3)} = 0.684$, $F_{(3,12)} = 0.082$, $P = 0.969$. For assemblage composition, two-way analysis of similarity (ANOSIM) on untransformed data gave the following results: $R_{light} = -0.092$, $P_{light} = 0.797$, $R_{scour} = -0.022$, $P_{scour} = 0.509$). The average pre-manipulation kelp density was 9.0 ± 0.640 kelps m^{-2} (mean ± SE, $n = 16$). The foliose algal assemblage was typically made up of 20% *P. lucida* and 5% *Rhodymenia sonderi*. Quadrats also contained large proportions of sand (20%), ascidians (10%) and encrusting algae (40%).

Light manipulations

Light was manipulated by deploying a steel mesh horizontally over each plot. The mesh was 1 m^2 in size and made of 5 mm steel rods in a 10×10 cm mesh. It was suspended approximately 15–20 cm above the substratum by attaching it to vertical steel rods anchored in each corner of the plot. The mesh was covered with plastic sheeting to manipulate light conditions within the plot. In high-light treatments, the mesh was covered with clear plastic sheeting, while in low-light treatments, dark plastic was used. Three slits each 30 cm long were haphazardly cut into the plastic sheets to allow the penetration of light flecks. The plastic sheeting was cleaned or replaced at least once every 2 weeks to prevent fouling from affecting the light climate. The effectiveness of light manipulation was assessed in an experiment using similar manipulations. It was found that there was no significant difference in light levels between dark plastic and kelp canopy. Similarly there was no difference in light levels between clear plastic and areas devoid of a canopy (Wernberg-Moller 2002).

Thallus scour manipulations

Thallus scour was simulated by hanging strips of transparent, heavy-duty PVC plastic sheeting (termed "tails") vertically from the steel mesh described above. Tails were made of food grade PVC approximately 35 cm long, 5 cm wide and 2 mm thick and were evenly distributed over the mesh. The tails were haphazardly placed in two orientations so that they scraped over the substratum when swell passed over. The high-scour treatments contained 60 tails and the low-scour treatment had 60 squares of the same PVC to serve as a control for any release of chemicals from the PVC. These squares, measuring 5×5×0.2 cm, were put into five groups of twelve and distributed evenly throughout the substratum of the plots.

The effectiveness of thallus scour manipulations was tested with clod cards (Muus 1968; Doty 1971). Two cards were randomly deployed per treatment, with three plaster cubes [$CaSO_4$ with latex paint (1.5 kg plaster, 300 ml paint, 150 ml water)] on each card. Thallus scour was measured as the average percentage loss of plaster per card under the assumption that differences in plaster loss due to differences in water motion and sediment scour were negligible relative to the amount lost due to thallus scour. The tails proved to be effective in scouring the substratum (For two-way, fixed factor ANOVA, Cochran's $C = 0.617$, $C_{crit(0.05,4,1)} = 0.906$; $F_{light\ (1)} = 3.573$, $P_{light} = 0.199$; $F_{scour\ (1)} = 65.092$, $P_{scour} = 0.015$, $F_{interaction\ (1)} = 7.409$, $P_{interaction} = 0.113$). Plaster lost from clod cards was not significantly affected by light treatments.

Sampling and data analysis

To quantify the changes in the foliose algal assemblage at the end of the experiment, all foliose algae within the central 0.25 m^2 of each plot were harvested. Samples were returned to the laboratory for identification using keys of temperate Australian algae (Womersley 1984, 1987, 1994, 1996, 1998; Huisman and Walker 1990; Huisman 2000). Dry weights of each taxon were determined after drying at 75°C for 72 h.

Dry weights of the foliose assemblage from treatment combinations were square-root transformed to reduce asymmetrical influence of the dominant species (Clarke and Gorley 2001), before Bray-Curtis similarities were calculated for each pair of samples and the resulting data matrix was used to generate a non-parametric multidimensional scaling (MDS) plot. A two-factor crossed non-parametric multivariate ANOVA was used to test whether assemblage composition differed significantly between treatment combinations (Anderson 2001). Similarity percentages (SIMPER) analysis was performed on the raw data to determine which species were the primary causes of the pattern observed in the MDS plot.

Species richness, total biomass, dominance (Berger-Parker index) and diversity (Shannon-Wiener index) were calculated for each treatment combination (Magurran 1988). Data were tested for homogeneity of variances using Cochran's *C*-test before a two-way, fixed-factor ANOVA was performed on each of these variables to determine if there were any significant differences ($P < 0.05$) between treatment combinations.

Photobiological investigations

Experimental design

Photobiological investigations were undertaken to determine the extent of photoacclimation in the three species *R. sonderi*, *P. lucida* and *Chauviniella coriifolia*. These species were chosen as they were all Rhodophtya and occurred both under kelp canopies and in gaps between canopies. In addition, these species (*R. sonderi* in particular) are very common components of the macroalgal assemblage associated with kelps throughout southwestern Australia (Wernberg et al. 2003b) and played a significant role in forming the patterns identified in the manipulative experiment (Table 1).

The photobiological state of these three species was examined in relation to the light climates underneath and outside a kelp canopy by estimating thallus photon absorption, maximum electron transport rate (ETR_{max}) and light-limited photosynthetic electron transport rate of light harvesting units (α). Causality of the observed patterns in photobiology was inferred from changes in the light use efficiency (quantum yield) of *R. sonderi* transplanted into the different light climates. *R. sonderi* was chosen for transplantation because it displayed the greatest change in photobiological state in relation to light climate.

Thallus absorption

To test for photoacclimation, 20 specimens each of *P. lucida*, *R. sonderi* and *C. coriifolia* were collected, 10 from underneath and 10 from outside the kelp canopy. Specimens were kept cool and in darkness as they were transported back to the laboratory. Thallus absorption was measured by placing a piece of epiphyte-free thallus from the apical part of the alga between an actinic light source and a light sensor [a diving pulse amplitude modulated (PAM) sensor], and recording the light transmitted through the thallus. Under the assumption that reflection from the thallus surface was negligible, absorption was calculated as:

$$\text{Absorption} = 1 - (\text{transmitted light}/\text{ambient light})$$

Thallus absorption data were tested with a two-way ANOVA using canopy (outside or underneath) and species (*P. lucida*, *R. sonderi* and *C. coriifolia*) as fixed factors. Variance was found to be heterogeneous with Cochran's *C*-test (Cochran's $C = 0.480$, $C_{crit(0.05,6,9)} = 0.368$). Log transformation of the data failed to correct the heterogeneity of variances, so the raw data were used in the analysis (Underwood 1997).

Table 1 Similarity percentages (SIMPER) analysis of the foliose algal assemblage at the end of the experiment. Biomass in grams

Species	+Light Biomass	−Light Biomass	Diss/SD[a]	Contribution (%)	−Light Change
Pterocladia lucida	2.45	7.06	1.45	37.69	Increased[b]
Rhodymenia sonderi	2.59	2.61	1.12	15.10	Increased[b]
Rhodopeltis australis	0.69	1.51	0.59	12.66	Increased[b]
Ulva spp.	1.61	0.39	1.26	12.37	Decreased[c]
Curdiea obesa	0.81	0.00	0.64	4.85	Decreased[c]
Chauveniella coriifolia	0.32	0.27	0.91	3.20	Decreased[c]

[a] Diss/SD denotes dissimilarity divided by standard deviation, and indicates the consistency of the contribution; species are ordered according to decreasing Diss/SD

[b] Increased abundance under low-light conditions

[c] Decreased abundance under low-light conditions

Light curves

To demonstrate the extent of photoacclimation, light curve parameters were determined for *P. lucida*, *R. sonderi* and *C. coriifolia* from underneath and outside the kelp canopy. In order to estimate ETR_{max} and α for all three species, three rapid light curves (RLC) were generated in situ for each species under high (more than four stipes per 0.25 m^2) and low kelp density (fewer than two stipes per 0. 25 m^2). These densities have been shown to have significantly different light climates (Wernberg-Moller 2002). Tissues sampled were dark-adapted for 10 min before RLCs were taken to allow photosynthetic reaction centres to oxidise. All RLCs were generated in a random order during the late morning (1000–1200 hours) to minimise the influence of diurnal rhythms in photosynthetic performance (Sagert et al. 1997; Hader et al. 2001). Sampling was done during the summer at the site used for the manipulation experiment and was repeated over 3 days (26 February, 5 March and 20 March) using different individuals on each day.

RLCs were measured using an underwater PAM fluorometer [Diving PAM (Walz, Germany)], using standard procedures (Beer and Bjork 2000; Beer et al. 2000, 2001; Franklin and Badger 2001). From preliminary trials, an illumination interval of 30 s was determined as the shortest interval that would generate replicable results. In order to obtain an accurate measurement of light-limited photosynthetic rate, the actinic light intensity was set to achieve approximately five values below the saturating irradiance. Since battery power strongly affects actinic light intensity, the light intensity was re-calibrated after every nine RLC recordings.

RLCs were generated by plotting the electron transport rate (ETR) against the actinic light intensity. ETRs were calculated using the thallus absorption values obtained in the previous investigation. Non-linear curves were fitted using the software MacCurveFit 1.2.2 (Raner 1996), applying the inverse tangential equation of Jassby and Platt (1976):

$$ETR = (ETR_{max}) \times [\tanh(\alpha I/ETR_{max})]$$

where I is the actinic light intensity.

Rhodymenia sonderi transplantation

The dominant foliose alga *R. sonderi* was transplanted from underneath the canopy to outside the canopy to test for differences in photobiological state. Maximum quantum yield measurements were also made on ten *R. sonderi* individuals underneath the canopy to characterise the photobiological state of the population before transplantation. Twenty specimens were collected from under the canopy for transplantation with ten specimens transplanted outside the canopy and an additional ten specimens transplanted back underneath the kelp canopy to serve as procedural controls. Specimens were transplanted by detaching a piece of the limestone reef including the alga with a chisel and anchoring it in the appropriate location by fixing it to a dive weight (1.5 kg of lead) with double-sided velcro ("One-wrap 330").

Yield measurements were made with a Diving PAM after dark adapting the algal tissues for a minimum of 10 min. All measurements were made within 1 h to minimise the influence of diurnal changes in light climate on yield measurements. Ten days after transplantation, a single yield measurement was made in situ on each transplant.

Yield data were analysed with an a priori planned comparison of the before-transplant condition with the procedural control treatment and that group with the experimental treatment, using Scheffe's test (Zar 1999). Data were found to have homogeneous variances using Cochran's C-test (Cochran's $C=0.542$, $C_{crit(0.05,3,9)}=0.617$). Some transplants were lost, reducing the sample size to seven and nine in the control and experimental treatments respectively.

Results

Manipulations of light and thallus scour

The non-metric MDS plot separated light treatments along the horizontal axis but failed to distinguish between thallus scour treatments (Fig. 1). The non-parametric multivariate ANOVA confirmed that the assemblage composition differed significantly between light treatments but not scour treatments and there was no interaction effect between light and scour (Table 2). Assemblage structure differed between light treatments because of the greater biomass of *P. lucida*, and *R. sonderi* and lower biomass of other species such as *Ulva* spp. and *C. coriifolia* under low-light conditions (Table 1).

Diversity was significantly lower in low-light treatments (Fig. 2a, Table 3). This change in diversity was associated with a significantly higher Berger-Parker index, as *P. lucida* and *R. sonderi* dominated in the low-light treatments (Fig. 2b, Table 3). Total biomass and species richness showed no consistent trends and differences between treatment combinations were non-significant.

Photobiological investigations

Thallus absorption

Thallus absorption varied significantly among species of foliose algae and between areas with and without a canopy (For two-way, fixed factor ANOVA, Cochran's $C=0.480$,

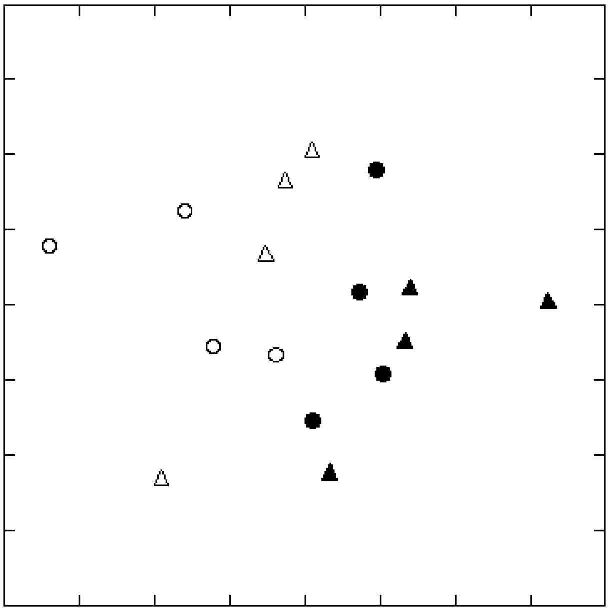


Fig. 1 Non-metric multidimensional scaling (MDS) ordination of square-root transformed biomass data of foliose algal assemblage samples (stress = 0.13). *Open symbols* denote high-light treatment, *closed symbols* denote low light. *Circles* represent low-scour treatment and *triangles* represent high scour. Separation of light treatments occurs along the horizontal axis. Axes refer to level of similarity

$C_{\mathrm{crit}(0.05,6,9)} = 0.368$; $F_{\mathrm{species}\ (2)} = 9.545$, $P_{\mathrm{species}} > 0.001$; $F_{\mathrm{canopy}\ (1)} = 35.501$, $P_{\mathrm{canopy}} > 0.001$; $F_{\mathrm{interaction}\ (2)} = 2.639$, $P_{\mathrm{interaction}} = 0.081$). In all three species, thallus absorption was greater in low-light conditions under the canopy than in high-light conditions outside it. The greatest difference in absorption between algae underneath a canopy and in gaps in the canopy was observed in *P. lucida,* with algae underneath the kelp canopy absorbing 11% more of the incidental light than their counterparts in the open patch. For *R. sonderi* and *C. coriifolia*, the difference in thallus absorption was 5% and 7% respectively (Fig. 3).

Light curves

All three species had higher $\mathrm{ETR_{max}}$ values for individuals in high-light conditions under a sparse canopy than for those in dark conditions under a dense canopy (Fig. 4) except for *C. coriifolia* on 5 March. On the last two sample dates, differences in $\mathrm{ETR_{max}}$ were greater for *R. sonderi* and *P. lucida* than for *C. coriifolia*. For all

Table 2 Two-way, fixed factor (light, scour) non-parametric multivariate analysis of variance (ANOVA) of Bray-Curtis dissimilarity of square-root transformed foliose algal assemblage data at the end of the experiment

	df	Mean square	*F* ratio	*P*
Light	1	4,151	3.623	< 0.001
Scour	1	1,030	0.899	0.527
Scour×Light	1	1,248	1.089	0.370
Error	12	1,145		

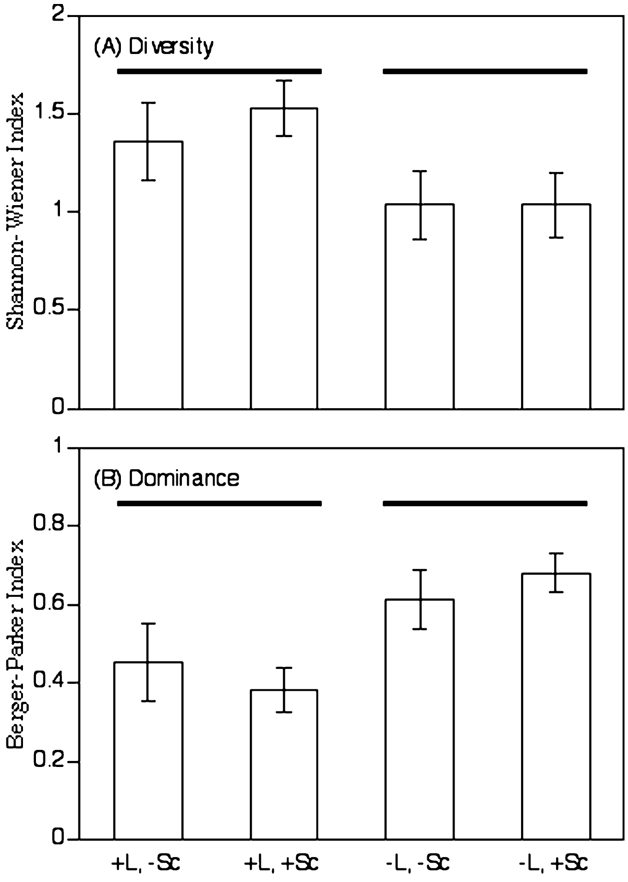


Fig. 2 **A** Diversity (Shannon-Wiener index) of the foliose assemblage in treatment combinations. **B** Dominance (Berger-Parker index) of the foliose assemblage in treatment combinations. Values shown are means ± SE, $n = 4$. *L* denotes light, *Sc* denotes thallus scour, + indicates a high level of a factor, - indicates a low level of a factor. *Horizontal lines* refer to treatments which are not significantly different at $P = 0.05$

Table 3 Two-way, fixed factor (light, scour) ANOVA for the Shannon-Wiener diversity index of assemblage samples (Cochran's $C = 0.320$, $C_{\mathrm{crit}(0.05,4,3)} = 0.684$) and the two-way, fixed factor (light, scour) ANOVA for the Berger-Parker dominance index (Cochran's $C = 0.453$, $C_{\mathrm{crit}(0.05,4,3)} = 0.684$)

	df	Mean square	*F* ratio	*P*
Diversity (Shannon-Wiener index)				
Light	1	0.674	5.741	0.034
Scour	1	0.028	0.236	0.636
Scour×Light	1	0.027	0.231	0.64
Error	12	0.177		
Dominance (Berger-Parker index)				
Light	1	0.206	9.819	0.009
Scour	1	< 0.001	0.001	0.974
Scour×Light	1	0.190	0.908	0.359
Error	12	0.021		

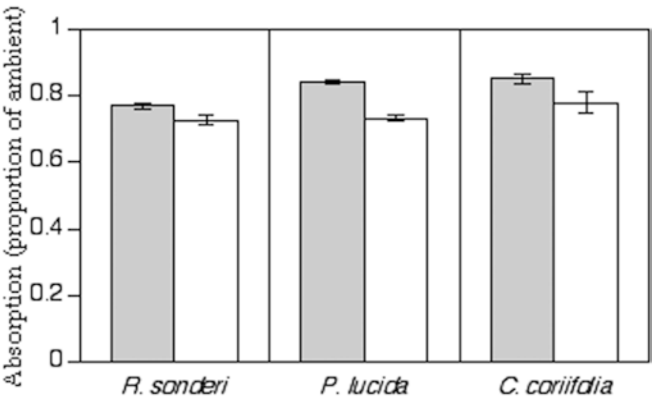


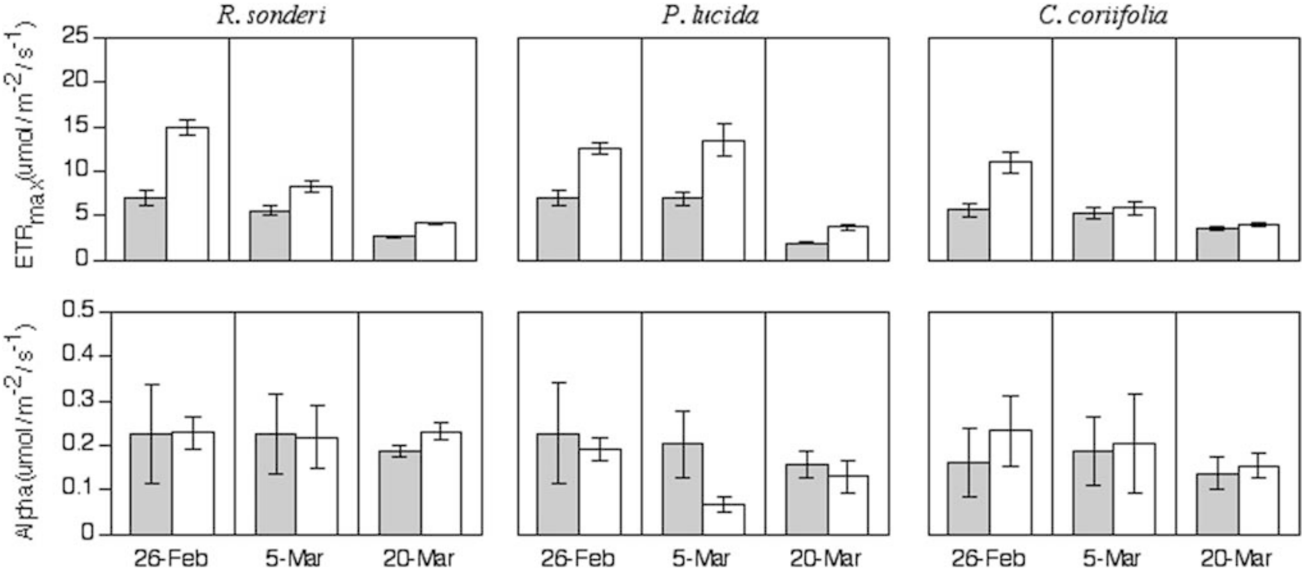
Fig. 3 Thallus absorption of *Rhodymenia sonderi*, *Pterocladia lucida* and *Chauviniella coriifolia* underneath (*shaded columns*) and outside (*unshaded columns*) an *Ecklonia radiata* kelp canopy. Values shown are means ± SE, $n = 10$, except for *C. coriifolia* outside the canopy where $n = 7$

species there were no significant differences in α except on 5 March for *P. lucida* and on 20 March for *R. sonderi*.

Rhodymenia sonderi transplantation

There was a significant change in the photobiological state of *R. sonderi* when transplanted from underneath to outside a kelp canopy. After transplantation, *R. sonderi* in the control treatment had a yield of 0.408 ± 0.012 (mean ± SE, $n = 7$) which was not significantly different from the yield of 0.460 ± 0.026 (mean ± SE, $n = 10$) in algae before transplantation ($P = 0.05$, $S_{\alpha} = 2.987$, $S = 1.551$). The transplants placed outside the canopy had a significantly lower mean yield of 0.330 ± 0.021 (mean ± SE, $n = 9$; $P = 0.05$, $S_{\alpha} = 2.987$, $S = 3.51$).

Fig. 4 Photosynthetic parameters for *R. sonderi*, *P. lucida* and *C. coriifolia*. Maximum electron transport rate (ETR_{max}) estimates appear in the *upper row* and light-limited photosynthetic electron transport rate (α) estimates appear in the *lower row*. Note the different scales for ETR_{max} and α graphs. High canopy densities (more than four stipes per $0.25m^2$) are represented by *shaded columns*. Low canopy densities (fewer than two stipes per $0.25m^2$) are represented by *unshaded columns*. Columns are paired according to sample date, chronologically ordered from left to right. *Error bars* ± 1 SE



Discussion

Overview

Our goal was to explore what mechanisms allowed an *E. radiata* canopy to influence its associated foliose algal assemblage. We tested whether light and thallus scour, in a wave exposed location, had independent and/or interactive effects on the foliose algal assemblage. We also investigated whether differences in the photoacclimative capacity between foliose species could explain how a reduction in the light levels results in changes in the composition of the foliose algal assemblage. Modification of light, but not thallus scour, resulted in a significant change in the species composition of the foliose algal assemblage. Reduced light levels were associated with a shift in assemblage composition, with greater dominance (as biomass) of *P. lucida* and *R. sonderi* under those conditions. Photobiological investigations into the three common foliose red algae, *P. lucida*, *R. sonderi* and *C. coriifolia,* indicated that they all photoacclimated under low-light conditions. We conclude that *P. lucida* and *R. sonderi* are able to dominate in low light found under a kelp canopy due to superior ability to photoacclimate. Other species such as *C. coriifolia* show reduced abundance in low-light environments, presumably due to inferior photoacclimative ability.

Light and thallus scour

In our experiment, light was found to be a significant factor in structuring the foliose algal assemblage. This is consistent with a large body of research from both *E. radiata* kelp beds of Australia and kelp forests in California (Pearse and Hines 1979; Dayton et al. 1984; Kennelly 1989; Wernberg-Moller 2002; Connell 2003a). It confirms that canopy shading is an important mechanism by which the kelp canopy influences the foliose algal assemblage in Marmion Lagoon.

In this experiment the composition of the foliose algal assemblage was not significantly affected by thallus scour. In spite of the differences in experimental design and exposure, our results are in general agreement with those of Kennelly (1989) who concluded that thallus scour was not an important influence on the algal assemblages in New South Wales. Although thallus scour was found not to play a significant role in determining the composition of the foliose algal assemblage in our experiment, it may exert more influence in other times and places. Thallus scour may play an important role in disturbing the foliose assemblage during such times as winter storms, when rough sea conditions increases the intensity of scouring (Kennelly 1989; Kiirikki 1996). Thus thallus scour may be better described as a ‘‘pulse’’ disturbance (Bender et al. 1984), which occurs at one point in time at semi-random intervals, than as a ‘‘press’’ disturbance, which operates constantly year-round.

The structure of the kelps may dictate whether thallus scour plays a role in structuring the foliose algal assemblage. Given that thallus scour decreases with stipe length in *E. radiata* (Kennelly 1989), it may be a less important factor in locations where a canopy of stipitate *E. radiata* exists, such as in New Zealand (Novaczek 1981). However, due to the high variability in kelp morphology at the local scale (Wernberg et al. 2003a), it may be that thallus scour has a highly localised and hence highly variable effect on the understorey assemblage.

Thallus scour may play an important indirect role in structuring the foliose algal assemblage by modifying the distribution and activity of invertebrates (Velimirov and Griffiths 1979; Konar 2000; Gagnon et al. 2003; Konar and Estes 2003; Connell 2003b). If thallus scour reduces the presence of sessile invertebrates underneath the canopy, this may leave more primary space to be occupied by foliose algae; however if thallus scour reduces the distribution or feeding activities of mobile invertebrates grazers such as sea urchins, then this effect may be more related to the recruitment of the kelp population than to the species composition of the foliose algal assemblage.

Photobiology

The differences in light climates underneath and outside the *E. radiata* canopy had a significant influence on the photobiological state of *R. sonderi*, *P. lucida* and *C. coriifolia*. The differences in $\mathrm{ETR}_{\mathrm{max}}$ and thallus absorption were consistent with photoacclimation in these species. Greater thallus absorption under low-light conditions confirmed visual evidence that the algae under the canopy had increased their pigmentation to capture more light. The changes in $\mathrm{ETR}_{\mathrm{max}}$, but not α, at low light levels suggests that these algae photoacclimate by increasing the number of photosynthetic units of a fixed size (Ramus 1981). A lower yield in the *R. sonderi* transplants suggest that the differences seen in the previous two investigations were directly related to canopy shading because a high yield under the canopy indicates a high light-use efficiency, which is reduced when transplanted outside the canopy. The rapid change in yield associated with the transplantation seen in this investigation is consistent with the rapid photoacclimation of *Pterygophora californica* following canopy removal (Watanabe et al. 1992).

The photoacclimation demonstrated by *R. sonderi*, *Pterocladia lucida* and *C. coriifolia* has also been observed in *Ulva lactuca* (Mishkind and Mauzerall 1980; Sand-Jensen 1988). By photoacclimating, the relative proportion of ambient light captured is increased, compensating for the overall reduction in light levels while still maintaining productivity (Gantt 1990). Shade-adapted *Botryocladia pseudodichotoma* in California have been found to be more productive than their sun-adapted counterparts (Heine 1983). In Marmion Lagoon, other algae such as *E. radiata* recruits, which are also found underneath the canopy (Kirkman 1981), may also photoacclimate sufficiently to maintain net carbon gains under low-light conditions.

There may be differences in the ability of different species of foliose algae to photoacclimate. In our investigations we found that *P. lucida* and *R. sonderi* photoacclimated more than *C. coriifolia*. Direct comparisons of the ability of different algal species to photoacclimate have rarely been reported, but differences in photoacclimative ability have been observed in red and green algae from different water depths and in response to seasonal changes in light climate (King and Schramm 1976; Ramus et al. 1976). Kuhl et al. (2001) found differences in the light adaptation index, $E_{\mathrm{k},}$ in three arctic brown algae. *U. lactuca* and *Porphyra umbilicalis* have also been found to photoacclimate in different ways, with the former increasing the number of photosynthetic units and the latter increasing the size of the photosynthetic units (Mishkind and Manuzerall 1980).

Differences in photoacclimative ability may provide a possible physiological explanation of the patterns observed in the manipulative experiment of this study and the species-specific canopy effects observed by Kendrick et al. (1999) and Wernberg-Moller (2002). The absence of some species in low-light conditions underneath the canopy may be due to their poor ability to photoacclimate, which translates into a poor tolerance of the low-light conditions. For example, of the three species investigated here, *C. coriifolia* photoacclimated the least and occurred in the lowest biomass under low-light conditions. The superior ability of *Pterocladia lucida* and

R. sonderi to photoacclimate may provide them with a competitive advantage in low-light environments (Carpenter 1990), possibly explaining their dominance of the assemblage under those conditions. The superior ability of *R. sonderi* and *P. lucida* to photoacclimate may also go some way to explain their high abundances in several otherwise biogeographically distinct kelp-associated algal assemblages along the southwestern coast of Australia (Wernberg et al. 2003b).

Overall, we conclude that *E. radiata* canopies in Marmion Lagoon primarily influence the foliose assemblage by modification of the light environment. Differences in the ability of individual species of foliose algae to photoacclimate offer a possible explanation as to how modification of light levels by a canopy of the small kelp, *E. radiata*, results in changes in species composition and abundances of members of the macroalgal assemblage.

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