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Canopy facilitates seaweed recruitment on subtidal temperate reefs

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Summary

1. Facilitation through physical stress amelioration has been largely overlooked in subtidal marine ecosystems, where abiotic gradients are perceived to be benign. However, seemingly subtle changes in marine environmental conditions can alter community structure across vast areas, and therefore, the type of interactions and any refuge provided by marine foundation species. This could have substantial implications for community organization.

2. We measured net recruitment rates of subtidal seaweeds under experimentally modified canopy densities, across 1000 km of coastline, to examine the nature of interactions between seaweed canopies and recruits.

3. Contrary to expectations, facilitation, as evidenced by higher recruitment under canopies, was observed throughout all conditions for *Scytothalia dorycarpa* and under partial canopies at three of four locations for *Sargassum* spp., whilst competitive interactions remained prevalent for *Sargassum* under closed canopies.

4. Supply side dynamics were also of major importance to recruitment success for *Scytothalia.* For *Sargassum*, the interaction strength between recruits and the canopy became increasingly positive towards lower latitudes, suggesting the canopy environment was mitigating stress across the latitudinal climate gradient.

5. *Synthesis.* Positive interactions and stress amelioration play an important and previously unrecognized role in determining the recruitment success and viability of seaweeds in subtidal marine ecosystems. These results challenge long held paradigms about the general importance of canopy competition and force a rethink of how seaweed interactions affect habitat resilience to disturbances in subtidal ecosystems.

Key-words: aquatic plant ecology, canopy competition, disturbance, kelp forest, ocean climate, plant–plant interactions, positive interactions, recruitment, stress gradient hypothesis, supply side ecology

Introduction

Plant facilitation through the alleviation of physical stress is an important driver of community structure across many ecosystem types (He, Bertness & Altieri 2013). Interestingly, however, it is considered to be relatively unimportant in the subtidal marine environment (Bulleri 2009; Sanford *et al.* 2009). Within subtidal kelp forests and seaweed beds generally, competition is instead considered to be the prevailing interaction in response to the physical environment, driving community structure and species richness (Schiel & Foster 2006; Bulleri 2009). Competition within subtidal canopies is thought to be driven primarily by the low light availability underneath the canopy, thereby preventing recruitment until natural gaps appear in the canopy (Reed & Foster 1984). This paradigm in subtidal ecology contrasts with many terrestrial and intertidal ecosystems where nurse plants facilitate the establishment of seedlings or propagules, particularly in harsh environments, by buffering them against high radiation, temperature, desiccation and salinity (Bertness & Yeh 1994; Tewksbury & Lloyd 2001; Castro *et al.* 2004; Gomez-Aparicio *et al.* 2004; Cuesta *et al.* 2010).

Facilitation in subtidal ecosystems has been widely observed in response to associational defence from grazing and predation (Hay 1986; Anderson *et al.* 1997; Stachowicz & Whitlatch 2005; Bulleri *et al.* 2011). Whilst associational defence can be an important structuring force in subtidal systems, the focus of this paper is the paradoxically uncommon role of plant–plant facilitation in response to the physical

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environment. Facilitation among subtidal plants (seaweeds and seagrasses) is thought to be rare due to the relatively benign physical environment underwater, compared to the extreme physical conditions of ecosystems, where facilitation is commonly observed, such as the intertidal (Stachowicz *et al.* 2008; Bulleri 2009). However, very few studies have tested plant facilitation in subtidal ecosystems (Bulleri 2009) and a long standing paradigm about the ubiquity of competitive interactions has developed from a few seminal papers which have demonstrated strong competitive effects, albeit across relatively small geographical areas (Dayton 1975; Dayton *et al.* 1984; Reed & Foster 1984; Kennelly 1987). Whilst absolute variation in the subtidal physical environment is often not as extreme as in many terrestrial or intertidal ecosystems, vulnerability to physical stress remains high. Organisms that are adapted to a narrow environmental range can experience stress and mortality following small absolute changes in conditions, due to the large relative change in the context of the historic regime of the organism (Tewksbury, Huey & Deutsch 2008; Peck, Morley & Clark 2010; Howells *et al.* 2013). Therefore, any alleviation of physical conditions even in relatively benign environments, such as subtidal systems, has the potential to promote facilitation (Holmgren & Scheffer 2010).

Subtidal temperate reefs are characterized by dense cover of perennial seaweed canopies (Schiel & Foster 1986) giving them the potential to promote positive interactions through physical stress amelioration. Positive interactions could be expected to prevail if the beneficiary species is experiencing physiological stress, and the benefactor can ameliorate the stress so that the net benefit is greater than the cost of living together (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003). The extent to which subtidal canopies ameliorate physical stress is likely to depend considerably on the structural characteristics of the canopy (Irving & Bertness 2009). Variation in canopy density has the capacity to alter the habitable space, resource availability and levels of stress amelioration provided by the benefactor species (Bruno & Bertness 2001; Irving & Bertness 2009; Bulleri *et al.* 2011). For kelps, canopy types can vary dramatically between floating canopies of giant kelp *Macrocystis pyrifera*, which greatly reduces light levels (Reed & Foster 1984) and can dampen wave energy (Jackson 1984), to the prostrate subsurface canopies (sensu Dayton *et al.* 1984) of species such as *Ecklonia radiata,* which also dramatically reduce light levels and are in constant contact with the benthos, scouring the bottom and reducing sediment load (Wernberg, Kendrick & Toohey 2005; Irving & Connell 2006).

Here, we examine the nature of interactions between subtidal seaweed canopies and their recruits under the prostrate kelp canopy of southwestern Australia. Given their stature, recruits are strongly influenced by the altered physical conditions under the canopy. We observed the net recruitment rates of two dominant genera of fucoids (*Scytothalia dorycarpa* and *Sargassum* spp.) within experimentally modified densities of *Ecklonia radiata* canopy across a 1000-km stretch of coast to examine the nature of interaction types throughout a system which has experienced a remarkably stable climatic and environmental evolutionary history.

Materials and methods

STUDY LOCATION AND SPECIES

The temperate coastline of southwestern Australia is characterized by the Leeuwin Current, a warm oligotrophic boundary current that extends down the west coast of the continent, providing a gradual 2–3 °C temperature gradient (Fig. 1), and relatively stable low-nutrient conditions throughout the region (Smale & Wernberg 2009; Wernberg *et al.* 2010). Moreover, continuous and extensive shallow (<15 m) limestone reefs provides consistent habitat conditions for seaweeds throughout the range. Reefs are covered by an extensive canopy of kelp, *Ecklonia radiata*, interspersed by the fucoids *Scytothalia dorycarpa* and *Sargassum* spp. (hereafter only mentioned by genus name). The relative abundance of *Scytothalia* and *Sargassum* changes throughout the coast, and the cover of the dominant canopy species, *Ecklonia,* remains constant (Table 1, Wernberg *et al.* 2011), thereby providing a consistent habitat for recruitment throughout the region.

Scytothalia is a cool adapted perennial species, confined to the western and southern Australian coastline between (approximately 30–40°S; Edgar 2000) and is vulnerable to elevated temperatures (Smale & Wernberg 2013) particularly during its early life stages (Andrews, Bennett & Wernberg 2014).Within the central and southern (poleward) end of its range, *Scytothalia* is a dominant component of the seaweed canopy, forming mixed or monospecific beds (Turner & Cheshire 2003), although it declines in abundance with increasing ocean temperature up the west coast of Australia (Wernberg *et al.* 2011). In contrast, *Sargassum* abundance is highest in the central location and is positively correlated to ocean temperatures (Wernberg *et al.* 2011). *Sargassum* has a broad geographical distribution, with the dominant west Australian species ranging from warm subtropical (26°S) to cool temperate climates (40°S). On the exposed reefs observed in the current study, *Sargassum fallax* and *Sargassum tristichum* are the most abundant *Sargassum* species within the canopy, whilst *Sargassum spinuligerum* is often found on the canopy margins. All three species share a similar distribution along the western coast of Australia and since it is not possible to differentiate between the recruits of these *Sargassum* species, all *Sargassum* recruits were recorded as *Sargassum* spp.

CANOPY DENSITY EXPERIMENT

Experiments were set up at four locations (300–400 km apart), along the coastline of southwestern Australia (Fig. 1). Within each location, three wave exposed sites (reefs >1 km apart) were haphazardly chosen between 8–12 m depth and with relatively flat topography. On each reef, 16 plots were marked within an area dominated by *Ecklonia* (Table 1). Six replicate plots of 100% and 60% canopy cover removal treatments (species were removed proportionally to their natural density; final densities of *Ecklonia* = 0 and 3.4 kelps $m^{-2} \pm 0.1$ SEM, respectively, $n = 4$ regions), and four control plots where no canopy was removed (density = 8.6 kelps $m^{-2} \pm 0.9$ SEM, $n = 4$ regions, no differences among regions, Wernberg *et al.* 2010) were set up in a haphazard arrangement at each site. Clearings ranged in size, with two replicate clearings of 2, 4 and 8 m radius established for each canopy removal treatment within each site. There was no significant difference in recruitment rates among the different plot sizes for *Scytothalia* (ANOVA, $F_{(2,141)} = 2.466$, $P = 0.069$) or

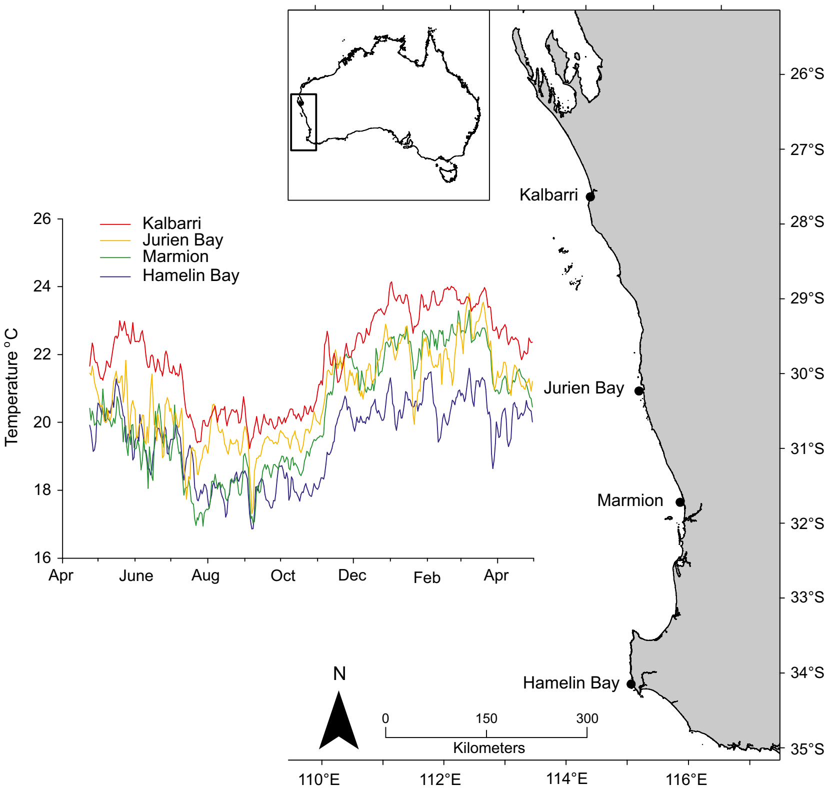

Fig. 1. Map of 4 study locations spaced between 28°S and 34 °S. Left panel illustrates the mean daily temperatures recorded within each of the four study locations from 2006 to 2007, during the time of the study. Data were averaged among in-situ Titbit temperature loggers deployed at three sites per location between 8 and 12 m depth.

Table 1. Mean habitat cover (percentage of the reef surface) of the dominant canopy species *Ecklonia radiata, Scytothalia dorycarpa*, *Sargassum* and other fucoids at the 12 study sites used in the study

Location	Site	*Ecklonia*	*Scytothalia*	*Sargassum*	Other fucoids
Hamelin Bay	HB1	71.2	8.7	0.8	4.7
	HB2	44.7	39.3	2.5	3.0
	HB3	64.6	19.4	1.4	0
Marmion	M1	55.1	0	0	0
	M2	56.0	11.6	6.8	0
	M3	64.8	2.7	1.8	0
Jurien Bay	JB1	59.5	7.5	8.2	0
	JB2	40.6	15.6	14.7	0
	JB3	45.2	2.8	1.6	0
Kalbarri	K1	86.8	0	5.6	0
	K2	70.9	0	8.5	0
	K3	66.9	0	19.6	0

Sargassum (ANOVA, $F_{(2,141)} = 1.039$, $P = 0.350$); therefore, the three sizes were pooled for further analyses. A minimum distance of 4 m was maintained between the edges of adjacent plots. Canopy removal was performed in March 2006 by pulling kelps and other large seaweeds, thus mimicking dislodgment by waves (see Wernberg *et al.* 2010 for further details of experimental design). Following canopy removal, a scuba diver counted the number of macroscopic *Scytothalia* and *Sargassum* recruits (juvenile specimens >1 cm) within a 1 m radius (3.14 m^2) from the centre of each plot. *Scytothalia* and *Sargassum* recruits are easily identifiable to the naked eye even at this small size due to their distinct morphology. Recruits were counted immediately after implementing the disturbances and again 8 months after the initial disturbance. All counts were conducted by TW. Conspecific adult density (CAD) of both *Scytothalia* and *Sargassum* was estimated for each site by counting the density of adults in undisturbed 3.14 m^2 patches ($n = 4$). All measurements were within a 30 m radius of the canopy clearance treatments. Mean CAD values from the undisturbed patches within each site were used to calculate the relationship between CAD and net recruitment rates into the three habitat treatments for both *Scytothalia* and *Sargassum*. For commensurability with the CAD measurements, all plots within a canopy density treatment were pooled to the site level analysis.

STATISTICAL ANALYSES

Net recruitment was calculated by subtracting the recruits present in each plot at the time of disturbance from the total number of recruits in same plot after 8 months. For *Scytothalia*, the northern-most location (Kalbarri, 28°S) was not included in the analyses, as this location is beyond the species' range (Smale & Wernberg 2013) and no adults or recruits have ever been observed there (Wernberg, personal observation).

The effect of the canopy density treatment and CAD on the net recruitment rates of *Scytothalia* and *Sargassum* were tested by analysis of covariance (ANCOVA). CAD was treated as a covariate of net recruitment, and canopy density treatment was used as a categorical grouping factor. For both *Sargassum* and *Scytothalia,* the residual vs fitted values plot and the Q–Q plot indicated homogeneity of variances and normal distribution of the data, therefore no transformation took place. For *Sargassum*, there was also no interaction between the covariate and canopy density treatment, demonstrating homogeneity of the slopes among treatments. For *Scytothalia*, however, there was a significant interaction between CAD and the canopy density treatment, violating the assumptions of co-linearity, meaning that no further interpretation of the ANCOVA mode could take place. Instead, we used the Wilcox procedure (Wilcox 1987) to determine what levels of

CAD recruitment rates among canopy density treatments differed (Quinn & Keough 2002). To apply the Wilcox procedure, we used the software WILCOX.exe, developed by A. Constable (Quinn & Keough 2002).

To determine the relative importance of the various spatial and canopy factors in determining the rates of recruitment, the total variance and variance components associated with the factors, 'CAD', 'canopy density treatment', 'site' and 'location' were estimated for the net recruitment rates of *Scytothalia* and *Sargassum* using a linear mixed effects model in the lme4 package of R (Bates 2005; Version 3.01, R_Development_Core_Team 2013). The spatial factors were treated as random nested effects, with sites nested within location, whilst CAD and disturbance intensity treatment were each treated as random crossed effect. Variance components were determined by calculating the proportion of the total variance explained by each individual factor (following Bennett *et al.* 2011).

The relative interaction index (RII), proposed by Armas, Ordiales & Pugnaire (2004), was used to compare the nature and intensity (sensu Brooker *et al.* 2008) of interactions of *Scytothalia* and *Sargassum* recruits with the canopy among locations. The RII is calculated as RII = $(R_o–R_w)/(R_o+R_w)$, where R_o = recruitment survivorship without neighbours and R_w = recruit survivorship with neighbours. The RII ranges between −1 and 1 and presents a continuous scale for competitive ($-1 \leq x < 0$) and facilitative ($0 \leq x < 1$) interactions that is symmetrical around zero. Because the RII requires positive values for its calculation, the value of 'gross recruits' within each patch present after 8 months was used, instead of net recruitment, which was negative in some treatments. Gross recruitment displayed the same pattern as net recruitment, but provides a more conservative estimate of the differences in recruitment between canopy treatments (Appendix S1 in Supporting Information). An ANCOVA was used to assess the differences in RII between partial and closed canopies along the latitudinal gradient for both *Sargassum* and *Scytothalia* recruits. Latitude was treated as a covariate of RII, and canopy density treatment was used as a categorical grouping factor. For both *Sargassum* and *Scytothalia,* the residual vs fitted values plot and the Q–Q plot indicated homogeneity of variances and normal distribution of the data, therefore no transformation took place. There was also no interaction between the covariate and canopy density treatment, demonstrating homogeneity of the slopes among treatments.

Results

EFFECTS OF ADULTS ON RECRUITMENT RATES

The canopy density treatment and conspecific adult densities (CAD) were strong determinants of recruitment for both *Scytothalia* and *Sargassum,* albeit with contrasting effects. Overall net recruitment rates of *Scytothalia* were highest in areas of partial (14.0 ± 2.4 mean ± SE) and closed canopy (7.8 ± 1.7), whilst lowest in no canopy patches (1.9 ± 1; mean ± SE; Fig. 2). In contrast, *Sargassum* displayed its highest recruitment rates in no canopy and partial canopy plots (17.2 ± 3 and 18.3 ± 2.7 mean ± SE respectively), whilst significantly lower rates of recruitment were observed in closed-canopy patches (2.9 ± 1.94; Fig. 2, Table 2). Partial and no canopy patches did not differ. The minimal adequate model for *Scytothalia* recruitment showed a strong positive relationship between recruitment rates and CAD in the surrounding canopy ($F_{(5,21)} = 19.86$, $P < 0.001$, adjusted $R^2 = 0.78$). CAD and the canopy density treatments showed a significant interaction (Table 2) whereby recruitment rates approached zero for all disturbance treatments at low adult densities, but increased more steeply on reefs with moderate to high adult density (Fig. 3). Post hoc tests using the Wilcox procedure revealed that recruitment rates were significantly higher in partial canopy plots than in no canopy plots, at adult densities above four adults per 3.14 m^2, whilst below this density, recruitment rates of all three disturbance treatments declined towards zero. The minimal adequate ANCOVA model for *Sargassum* recruitment rates demonstrated a significant positive relationship between *Sargassum* adult density and recruitment rates ($F_{(3,32)} = 10.64$, $P < 0.001$, adjusted $R^2 = 0.45$). Overall CAD explained 42.5% of total variation in *Scytothalia* recruitment rates, whilst the canopy density treatments explained 21.4% of total variation (Table 3). For *Sargassum,* the canopy density treatments explained 18.8% of the total variation in *Sargassum* recruitment rates, whilst CAD only explained 6.5%.

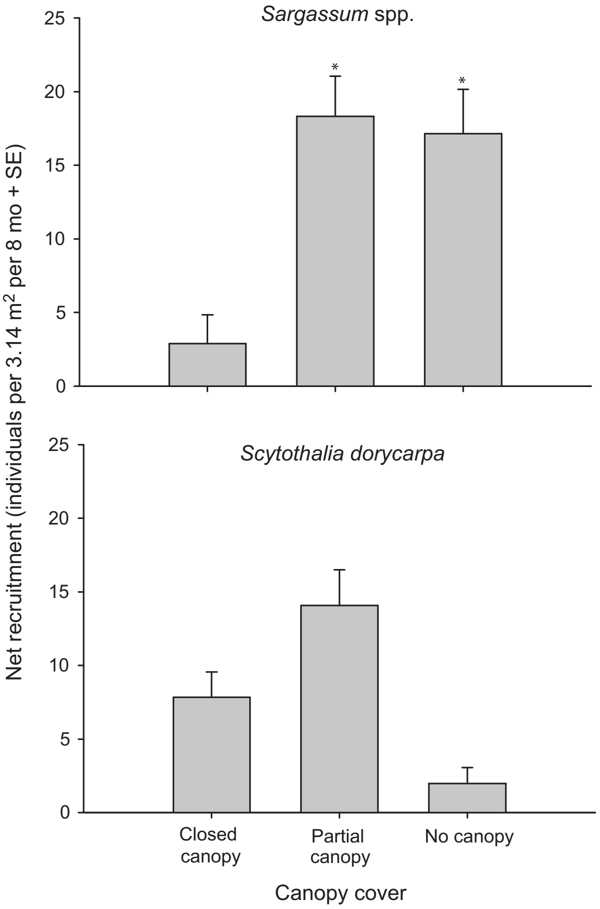

Fig. 2. Net recruitment patterns for *Sargassum* and *Scytothalia* under the three canopy density treatments. Results are averaged among latitudinal locations. * No difference ($P > 0.05$).

REGIONAL VARIATION IN INTERACTIONS

The interaction strength for *Scytothalia,* as evidenced by the RII scores, remained positive at all observed sites and did not

Table 2. Results of minimum adequate ancova model, testing the effects of canopy on net recruitment rates for *Scytothalia* and *Sargassum.* Conspecific adult density (CAD) was used as a covariate and the canopy density treatments as a categorical predictor. 'No canopy', 'Closed' and 'Partial' refer to three canopy density treatments

		Estimate	SE	*t*-value	Pr(>|*t*|)
Scytothalia	(Intercept)	2.437	2.858	0.853	0.403
	No canopy – closed	−2.753	4.042	−0.681	0.503
	Closed – Partial	1.634	4.042	0.404	0.690
	Partial – No canopy	4.388	4.042	1.086	0.290
	CAD	2.369	0.638	3.711	0.001
	No canopy – closed X CAD	−1.468	0.903	−1.627	0.119
	Closed – Partial X CAD	2.093	0.903	2.319	0.030
	Partial – No canopy X CAD	3.562	0.903	3.945	<0.001
Sargassum	(Intercept)	−3.720	3.811	−0.976	0.336
	No canopy – closed	14.253	4.965	2.871	0.007
	Closed – Partial	15.415	4.965	3.105	0.004
	Partial – No canopy	1.162	4.965	0.234	0.816
	CAD	24.778	5.547	4.467	<0.001

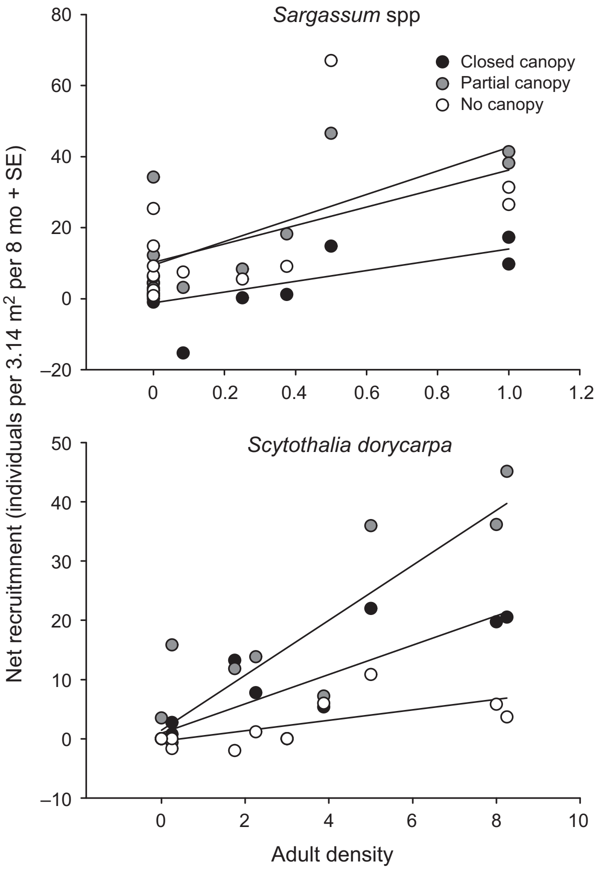

Fig. 3. Relationship between net recruit survivorship and conspecific adult density (CAD) under the three canopy density treatments. Note the different *y*-axis scales for *Scytothalia* and *Sargassum.*

significantly change among latitudes, or between partial and closed-canopy plots (Fig. 4 and Table 4). In contrast, the RII for *Sargassum* recruits was significantly higher for partial canopies than for closed canopies throughout the latitudinal range (Table 4). Three of the four latitudes recorded positive RII scores, indicating a net facilitative interaction, for partial canopies, whereas all four latitudes recorded negative RII scores under closed canopies (Fig. 4). RII scores for *Sargassum* displayed an upward trajectory towards warmer latitudes, despite differences among latitudes remaining marginally non-significant ($P = 0.053$, Table 4).

Discussion

Our study has demonstrated that positive plant interactions can play an important role for recruitment processes in subtidal ecosystems and that the strength and direction of these interactions differ between beneficiary species and in response to benefactor density. *Scytothalia* recruits were strongly facilitated at all locations, under both closed and partial canopy. *Sargassum* recruits also displayed positive interactions under partial canopy in three of the four locations, however, in contrast to *Scytothalia*, displayed a net negative interaction with the closed canopy. The interaction strength between *Sargassum* recruits and the canopy displayed an upward trajectory towards lower latitudes, whereby closed-canopy interactions became less competitive and partial canopy interactions, increasingly positive, suggesting the canopy environment might mitigate stress across broad scale latitudinal climatic gradients. For *Scytothalia,* supply side dynamics were also of major importance to recruitment success. Even in areas of closed canopy, if *Scytothalia* adult densities were low, recruitment approached zero. The close relationship between *Scytothalia* recruitment and adult densities highlights the likely difficulty for *Scytothalia* to recover from large-scale disturbances such as the 100-km range contraction in the wake of the 2011 marine heatwave (Smale & Wernberg 2013), because recruits are dependent on established adult populations to survive and the adult population relies on new recruitment to recover.

The positive interactions observed between recruits and seaweed canopies contrasts with the prevailing notion that competition alone drives plant interactions in response to physical stress in subtidal marine system (Dayton *et al.* 1984; Reed & Foster 1984; Kennelly 1987; Kendrick 1994; Emmerson & Collings 1998). Whilst facilitation through

Table 3. Results of linear mixed effects model fit by restricted maximum likelihood (REML), indicating variance components. Untransformed net recruitment rates analysed as a function of four random effects. *Sargassum* and *Scytothalia* were analysed separately. CAD is 'conspecific adult density'

	Variance		SD		% Total variance	
Groups	*Scytothalia*	*Sargassum*	*Scytothalia*	*Sargassum*	*Scytothalia*	*Sargassum*
Site(Latitude)	0.00	0.00	0.00	0.00	0	0
CAD	64.52	23.00	8.03	4.80	42.45	6.52
Latitude	6.58	175.16	2.57	13.24	4.33	49.68
Canopy density	32.52	66.34	5.70	8.15	21.39	18.82
Residual	48.37	88.10	6.95	9.39	31.82	24.98

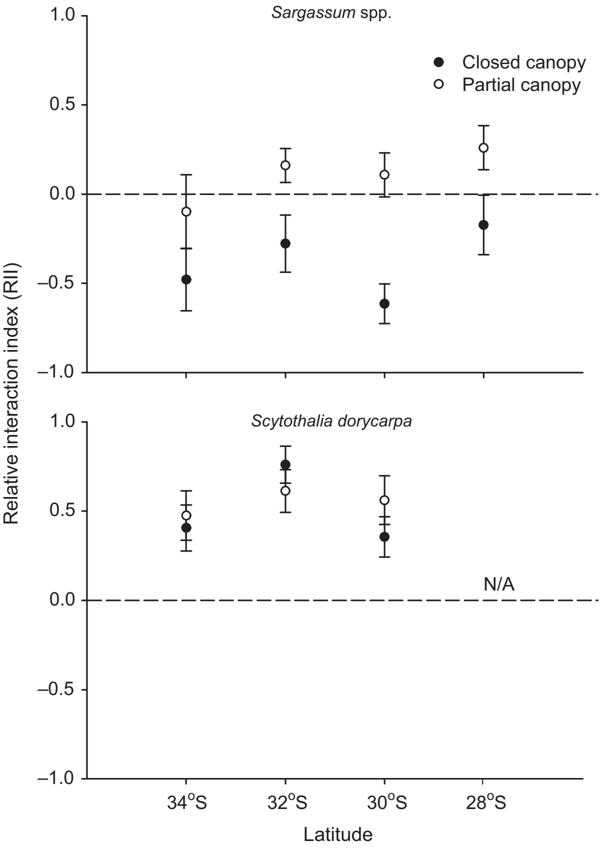

Fig. 4. Mean relative interaction index (RII) values for *Sargassum* and *Scytothalia* recruit–canopy interactions for two canopy density treatments across four latitudinal locations.

associational defence has been widely reported in subtidal systems, few studies have demonstrated facilitation in response to the physical environment (see Bulleri 2009 for a review). Previous studies have suggested that the higher light availability in canopy-free patches was the cause of higher recruitment and survivorship into these areas than adjacent canopy patches. The higher within-canopy recruit survivorship patterns observed here, however, suggest that the within-canopy light environment might be favourable, particularly for *Scytothalia* and for both species under a partial canopy. The high wave exposure of our study sites could mean that constant light-flecking within the canopy increases the photosynthetic efficiency of recruits, compared to no canopy steady state light conditions, as observed previously for several species (Greene & Gerard 1990; Wing & Patterson 1993; Kübler & Raven 1996; Raven & Hurd 2012). These conditions contrast with the very sheltered and dense surface canopy which induced a strong negative canopy–recruit interactions in some previous studies (e.g., Reed & Foster 1984), potentially due to comparatively low light-flecking and stable low light canopy environment in those systems.

Contributing explanations for the observed recruitment patterns could relate to the physical abrasion experienced within the canopy environment. *Scytothalia* is a robust leathery species, in comparison to *Sargassum* which has weaker attachment and has adapted to fragment easily as a means of dispersal (Thiel & Gutow 2005; Schiel & Foster 2006). Dislodgement by the highly abrasive environment might have contributed to the differences in closed-canopy recruitment between *Scytothalia* and *Sargassum.* The other feature of the abrasive canopy environment, which may have favoured *Sargassum,* however, is its effect on epiphytic loading. Reduced abrasion in canopy-

Table 4. Results of ancova model testing the relative interaction index (RII) of *Scytothalia* and *Sargassum* recruits against the 'Canopy density treatment' and using 'Latitude' as a covariate

		Df	SS	MS	*F*	Pr(>*F*)
Sargassum	Latitude	1	1.018	1.018	3.824	0.053
	Canopy density treatment	1	5.836	5.836	21.918	<0.001
	Residuals	93	24.763	0.266		
Scytothalia	Latitude	1	0.054	0.0538	0.277	0.600
	Canopy density treatment	1	0.032	0.032	0.166	0.685
	Residuals	69	13.386	0.194		

free habitats promotes epiphytic growth which can greatly reduce the productivity and health of the individual (Kiirikki 1996; Stachowicz & Whitlatch 2005; Andersen *et al.* 2011). This mechanical defence could be indirectly linked to the positive trajectory in interaction strength (i.e. less negative and more positive for closed and partial canopies, respectively) between *Sargassum* recruits and the canopy, in warmer locations. Temperature is the only significant environmental factor to change among locations (Wernberg *et al.* 2010), and whilst the canopy is unlikely to directly ameliorate temperature stress in these highly dynamic environments, higher epiphytic loading at warm locations due to increased metabolic rates of the epiphytes and physiological stress of the recruits could have prompted a shift towards positive interactions with the canopy. Whilst physical stress amelioration is uncommon in subtidal systems, associational defences from herbivory are widespread (Hay 1986; Stachowicz & Hay 1999). However, herbivore impacts are relatively low along the temperate Western Australian coastline (Wernberg, White & Vanderklift 2008; Vanderklift, Lavery & Waddington 2009) and are therefore unlikely to have played a significant role in the shaping of the recruitment patterns observed in this study. Moreover, *Sargassum* is highly palatable by herbivores in other systems (Bennett & Bellwood 2011; Vergés, Bennett & Bellwood 2012), and therefore, *Sargassum* recruits would be expected to be targeted if herbivory was shaping the observed patterns of recruitment. However, overall *Sargassum* recruitment was higher in canopy-free areas, and no evidence of herbivory was observed further suggesting herbivores played an insignificant role in shaping the observed patterns.

The prevalence of positive interactions in plant communities provides multiple advantages to beneficiary species, beyond individual benefits of ameliorating stress. For instance, facilitation can extend the realized niche of a species beyond what is expected from its fundamental niche, that is physical tolerance limits (Bruno, Stachowicz & Bertness 2003). For *Scytothalia,* a cool temperate adapted species, facilitation by the canopy strongly assists recruit survivorship throughout the temperate west coast of Australia. For the supply side ecology of west coast populations, however, such dependence on canopy cover and high conspecific adult density for survival makes *Scytothalia* particularly vulnerable to disturbance events that cause a reduction in canopy cover. In 2011, a marine heatwave off the west coast of Australia caused a large reduction in total seaweed canopy cover (Wernberg *et al.* 2013) and 100% loss of *Scytothalia* across 100 km from Jurien Bay (Smale & Wernberg 2013). The strong relationship between *Scytothalia* recruitment with conspecific adult density and the canopy density treatments suggests that the recovery of *Scytothalia* in Jurien Bay will be very slow, if at all. Furthermore, given that the same canopy dependency is observed throughout its range along west coast of Australia, similar responses could be expected in other locations if major canopy loss was to occur. In contrast, *Sargassum* is likely to be a beneficiary of disturbance events and in fact may provide a crucial pathway for the re-establishment of canopy-dependent species such as *Scytothalia.* The propensity of *Sargassum* recruitment in canopy-free patches means that following large-scale canopy loss, *Sargassum* is likely to be quick to recover and by re-establishing canopy conditions provides a successional pathway for *Scytothalia* (Toohey, Kendrick & Harvey 2007).

A second advantage *Sargassum* has for re-establishment following disturbance events is its greater capacity for long distance dispersal, compared to *Scytothalia.* Both *Sargassum* and *Scytothalia* have a typical fucoid life cycle with relatively large zygotes which settle to the bottom quickly upon release from the adult plant and within metres of the parent (Kendrick & Walker 1995). Long distance dispersal therefore is largely dependent on detached, reproductive adult plants being washed further afield (Schiel & Foster 2006). *Sargassum* has a floating thallus making it capable of long distance dispersal via wind-driven rafts of reproductive adult tissue, enabling propagules to release and populate reefs tens of kilometres away from the original site. *Scytothalia* on the other hand has a negatively buoyant thallus and is dependent on wave motion and bottom currents for dispersal, limiting the distance propagules can travel. This trait may provide an explanation for the strong adult-recruit relationship observed for *Scytothalia*, whereby reefs with low densities of adult *Scytothalia* recorded almost no recruitment, whereas *Sargassum* recruitment was more even throughout.

Facilitation by foundation species leading to habitat provision and environmental modification is an important structuring process in communities. This study has demonstrated that facilitation through amelioration of physical stress can play an important role in subtidal marine systems, challenging the long held notion that only competition drives plant–plant interactions in response to physical stress in subtidal ecosystems. Strong facilitation was observed throughout all conditions for *Scytothalia*, under partial canopy in three out of four locations for *Sargassum,* whilst competitive interactions remained prevalent for *Sargassum* under dense closed canopies. The importance of facilitation in these reefs affects our understanding of the resilience of kelp forests and seaweed canopies, the feedbacks that might reinforce habitat loss in these systems and opens up exciting new directions to further explore the prevalence of facilitation in subtidal marine ecosystems.

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Data accessibility

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.72181 (Bennett & Wernberg 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Figures for the gross and net recruitment patterns respectively for *Sargassum* and *Scytothalia* under different canopy treatments across the four latitudinal locations.

Figure S1. Gross recruitment patterns.

Figure S2. Net recruitment patterns.