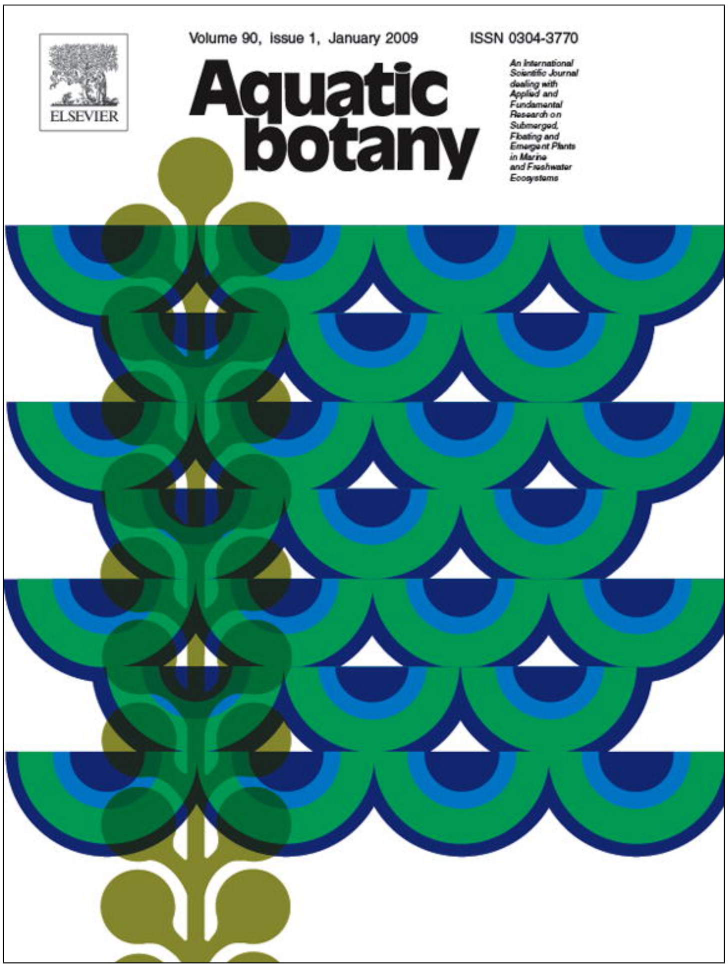
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Short communication

Spatial variation in juvenile and adult *Ecklonia radiata* (Laminariales) sporophytes

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ABSTRACT

Juvenile and adult sporophytes of *Ecklonia radiata* were counted on in-shore and off-shore reefs at Marmion (Perth, Western Australia), across spatial scales of kilometres, 10s of metres and metres. The position on in-shore reefs *vs.* off-shore reefs did not influence recruit and adult kelp density. There was considerable site-to-site (kilometres) variation in densities of recruits but not adults. The majority of variation in both recruit and adult densities was found between quadrats separated by a few metres. There was no relationship between abundance of recruits and abundance of adult sporophytes at any of the spatial levels of investigation, suggesting a decoupling of recruitment and canopy processes. The results emphasise the patchy nature of kelp canopy distribution and suggest that relatively small-scale processes, acting on scales of a few metres, are of primary importance in generating heterogeneity in the canopy of these kelps.

1. Introduction

Ecklonia radiata (C. Ag.) J. Agardh is a small kelp that often form dense beds on subtidal temperate reefs in the southern hemisphere (e.g., Wernberg et al., 2003a,b). Many kinds of disturbances, including storms (Kennelly, 1987), grazing (Andrew and Jones, 1990) and pathogens (Cole and Babcock, 1996), affect kelp beds on spatial scales of metres to kilometers. Disturbances are often age-selective, for example as grazing on juveniles (Anderson et al., 1997) or storm dislodgment of grown individuals (Dayton et al., 1984), and this may be a common cause of variation in population structure in kelp beds (Andrew and Jones, 1990; Markel and DeWreede, 1998). The predominance of age-specific mortality implies that populations with broad age-class distributions have higher resilience to perturbations because their risk of local extinction following a single disturbance event is reduced (Dayton et al., 1992). Hence, the spatial distribution of recruits and adults may reflect spatial variation in past disturbance events and may determine the ability of the canopy to withstand future disturbances and persist in space and time. Chronological age may be a poor ecological descriptor in macroalgal populations because physiology, reproduction and mortality often are more closely related to size (Chapman, 1986; Thomsen et al., 2004). Kirkman (1981, 1984) described three macroscopic life stages for *E. radiata*, two juvenile stages and one large adult stage. Stage 1 is the small (6.5–27 cm) recruit stage where the lamina is undifferentiated. Stage 2 (19–34 cm) is the large recruit stage where the lamina starts to develop primary laterals, and, stage 3 is the adult stage (>30 cm) where the thallus becomes fully differentiated into a large bushy complex of higher-order laterals.

This study asks the questions (1) what are the densities of juvenile (=recruit) and adult sporophytes? (2) Over what spatial scales do these densities vary? and (3) is there a link between densities of recruits and adults? Answers to these questions are ecologically significant because they are required to understand the dynamics of a species which exert a strong influence on reef communities (Connell, 2003; Toohey et al., 2004; Wernberg et al., 2005).

2. Methods

E. radiata sporophytes were counted on limestone reefs at Marmion (31°49.5 S 115°42.0 E) north of Perth in Western Australia. Sampling was stratified in-shore and off-shore in-shore of a line of high relief reefs because these areas represent different hydrodynamic environments (Wernberg and Thomsen, 2005). Three randomly selected sites were nested within each reef line. Sites were selected to have >60% *E. radiata* canopy cover and depths of 5–8 m (depth of maximum kelp abundance; kelp extend beyond 20 m in the area, Kirkman, 1984). Depths varied by ±1 m within a site and there were no apparent differences between reefs

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Table 1
Results of tests for differences in recruit and adult densities of *E. radiata* across reef lines, sites and plots

Source of variation	D.f.	MS	*F*	*p*	ω^2
Recruits					
Reef lines	1	1291	1.046	0.36	0.6
Sites (reef lines)	4	1234	13.30	≪**0.001**	37.8
Plots (sites)	24	92.8	1.665	**0.04**	6.1
Residual	150	55.8			55.5
Adults					
Reef lines	1	1.669	1.582	0.28	1.37
Sites (reef lines)	4	1.055	1.330	0.29	1.72
Plots (sites)	24	0.7931	1.852	**0.01**	12.0
Residual	150	0.4282			84.9

Recruits: no transformation, Cochran's test for normality: $C < 0.46$; $p > 0.05$.
Adults: $X^{0.5}$-transformed, Cochran's test for normality: $C < 0.48$; $p > 0.05$.
Significant p values (< 0.05) are highlighted in bold.

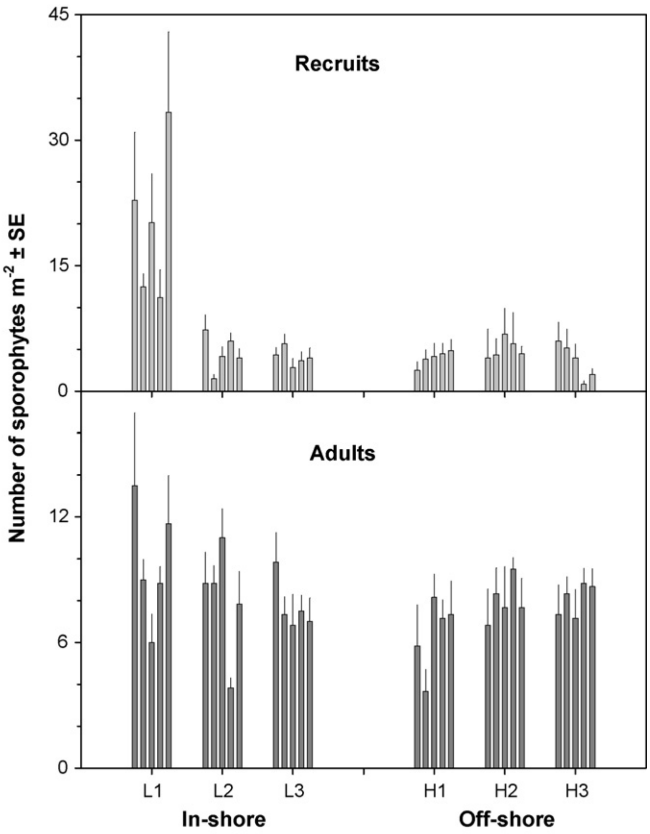

Fig. 1. Densities of recruit (stages 1 and 2) and adult (stage 3) sporophytes of *Ecklonia radiata* at Marmion. Each bar represents a plot ($n = 6$ quadrats; error bars = standard error) within a site. L1-3, and H1-3 are sites located on in-shore (low wave exposure) and off-shore (high wave exposure) reefs, respectively.

lines (i.e., in-shore *vs.* off-shore). Five random plots were nested within each site. Each plot was marked with a metal stake. In March 2000, late southern hemisphere summer, all sporophytes >2 cm were counted in six 1 m^2 quadrats, haphazardly placed within an 8 m radius of the stake marking each plot. Sites within reef lines were separated by 1–3 km, plots within sites by 10–30 m and quadrats within plots by a few metres. Prior to analysis with an all random factor fully nested ANOVA, data were checked for homogeneity of variances with Cochran's *C*-test and transformed if heteroscedastic ($p < 0.05$). Variance components were calculated for each level of the analysis and the magnitude of effect (ω^2) determined (Graham and Edwards, 2001).

3. Results

There were no differences in recruit (stage 1 and 2) or adult (stage 3) densities between off-shore and in-shore reef lines and this factor contributed less than 1.4% to the variance in sporophyte densities (Table 1). Recruit densities were significantly different among sites within reef lines because at five of the six sites there were 4–6 recruits m^{-2}, and at one in-shore site >15 recruits m^{-2} (Fig. 1). Consequently, sites within reef lines explained almost 40% of the total variance in recruit densities (Table 1). Recruit densities were also significantly different among plots within sites, but this level of nesting only explained 6% of the variance. The remaining 55% of the variance was contained in the residual, which corresponds to variation among replicate quadrats within plots. Densities of adult sporophytes ranged from 4 to 14 individuals m^{-2} in plots at all six sites (Fig. 1). Differences among plots within sites were statistically significant (Table 1) although these differences only accounted for 12% of the variance. Again, the residual (variation among quadrats within plots) accounted for almost 85% of the variance in density of adult kelp sporophytes.

There were no significant correlations between the abundance of recruit and adult sporophytes at any of the spatial levels of investigation in this study (Table 2).

4. Discussion

Reef line, the position off-shore and in-shore of a ridge of high relief reefs, did not influence the density of kelp sporophytes. This corresponds to previous findings from Marmion (Hatcher, 1989), and suggests that the difference in water motion across the reef line is too small to significantly affect the abundance of *E. radiata* at this time of the year. The survey was done at the end of summer, the calmest season where kelp abundance is at a peak (Wernberg and Goldberg, 2008), and it cannot be ruled out that kelp densities would differ between reef lines at other times characterised by stronger hydrodynamic forces.

The predominance of metre-scale variation in sporophyte densities indicates that small-scale post-dispersal processes determine the spatial distribution of *E. radiata*. For example, localised disturbances could affect individual adult sporophytes that are weakened by grazers (Markel and DeWreede, 1998). In contrast to adult sporophytes, recruit densities were patchily distributed on several spatial scales indicating that interactions between multiple processes may determine their distribution. This result contrasts that of Kennelly and Underwood (1992) who found *E. radiata* recruits to be the only major constituent of kelp bed communities to exhibit a consistent pattern of variation across several spatial scales. In addition to the large small-scale variation, sites (kilometres apart) also contributed substantially to variation in juvenile abundance. This finding matches patterns in South Australia where there was also large variation in recruitment of *E. radiata* among sites kilometres apart (Wernberg and Connell, 2008). In South Australia, however, recruitment at the site level was clearly related to the abundance of adult kelps. There were no obvious differences among the sites in Marmion and the distinctly

Table 2
Spearman's rank correlation between the densities of recruits and adult sporophytes at each of the spatial scales of investigation

	Spatial extent (m^2)	Spearman's, *r*	*p*	*n*
Sites	Several 100's	0.46	0.35	6
Plots	50	0.28	0.14	30
Quadrats	1	0.09	0.22	180

higher abundance of recruits at one site is either a product of an unknown stochastic event or relatively inconspicuous peculiarities of that site (e.g., slight variations in the rock or local circulation patterns).

Except at site L1, where recruits dominated the population, there were generally more adult (stage 3) than juvenile (stage 1 and 2) sporophytes. This is consistent with previous observations from Marmion (Kirkman, 1981; Hatcher, 1989), but contrasts reports from Goat Island in New Zealand where the smallest size classes dominate populations of *E. radiata* sporophytes (Schiel, 1990). Kelp canopies suppress the growth of recruits and increased recruitment and recruit growth often follow canopy removal (Kirkman, 1981; Dayton et al., 1984; Schiel, 1990). Such a mechanistic link between recruitment and adult canopy implies a negative relationship between recruit and adult density on small spatial scales (metres) (Johnson and Brawley, 1998). On the other hand, kelp propagules generally have limited dispersal distances and the vast majority of recruitment occurs within a few metres of the parental plants (e.g., Dayton et al., 1984). A positive relationship between canopy abundance and recruit density may therefore be expected over larger (>10s m–km) scales (Wernberg and Connell, 2008). There was no relationship between recruit and adult densities at any of the spatial scales investigated here. However, the link between recruitment and canopy density may not be easily detectable because post-dispersal processes such as high mortality rates of juveniles (e.g., by photo-stress, Toohey and Kendrick, 2007) may counter the transition of recruitment bursts into adult canopy (Johnson and Brawley, 1998). Only a very limited number of microscopic propagules develop to the macroscopic recruit stage (Kendrick and Walker, 1994) and only the few recruits necessary to maintain a constant adult population will develop further into adult sporophytes. Hence, the data indicate that there is a de-coupling of recruitment and canopy processes by the presence of post-dispersal mechanisms, acting on the gametophyte or embryonic sporophyte stage.

In conclusion, it appears that both recruit and adult sporophyte abundance at Marmion is controlled mainly by processes operating at small spatial scales (metres). It also appears that recruit and adult abundances are de-coupled in space.

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