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Persistence of sea urchin (*Heliocidaris erythrogramma*) barrens on the east coast of Tasmania: inhibition of macroalgal recovery in the absence of high densities of sea urchins

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Abstract

Sea urchin barrens occur commonly in temperate regions throughout the world and have significant implications for ecological processes on subtidal rocky reefs because they constitute areas of low productivity and diversity compared with habitats dominated by macroalgae. On the east coast of Tasmania, the occurrence of sea urchin (*Heliocidaris erythrogramma*) barrens in sheltered bays has additional implications in that they represent an important habitat of the introduced kelp *Undaria pinnatifida*. Identifying the factors responsible for ongoing maintenance of the barren habitat is essential in defining management options to promote recovery of native canopy-forming species. We used transplant experiments to investigate whether inhibition of recovery of native canopy-forming algae can occur in the absence of intense sea urchin grazing. High densities of native canopy-forming species successfully colonised paving blocks deployed in a dense algal bed adjacent to a sea urchin barren. Transplanting these paving blocks to plots on the barren from which sea urchins were removed resulted in >80% mortality of recruits after three months, and 100% mortality after seven months. The decline in macroalgal recruits on paving blocks transplanted to the urchin barren was associated with an increase in the cover and depth of sediment. A persistent cover of sediment also developed on paving blocks deployed on the urchin barren, where no native canopy-forming algal recruits were observed. While sea urchins are undoubtedly important in creating urchin barrens, our results suggest that other mechanisms can influence recovery of native canopy species. In sheltered and semi-exposed bays on the east coast of Tasmania, sedimentation appears to play a critical role in inhibiting early developmental stages of native macroalgae, thereby contributing to a positive feedback that acts to maintain the barren habitat.

Keywords: canopy-forming algae; persistence; sea urchin grazing; sediment; transplant.

Introduction

The occurrence of sea urchin 'barrens' characterised by high densities of sea urchins and low cover of foliose algae on rocky reefs has been widely reported from temperate regions across the globe (Lawrence 1975, Choat and Schiel 1982, Fletcher 1987, Chapman and Johnson 1990, Watanabe and Harrold 1991, Andrew and Underwood 1993, Hagen 1995, Sivertson 1997, Agatsuma et al. 2000, Shears and Babcock 2002). Urchin barrens are unproductive habitats compared to reefs dominated by seaweeds, with primary productivity ca. two orders of magnitude lower than comparable vegetated habitats (Chapman 1981).

In southeastern Tasmania, sea urchin 'barrens' dominated by the purple sea urchin *Heliocidaris erythrogramma* (Valenciennes) are a common feature of subtidal reefs in sheltered and semi-exposed waters. Two features of these barrens distinguish them from typical barrens elsewhere in the world (Johnson et al. 2004). Firstly, compared to other barrens supporting sea urchins of a similar size to *H. erythrogramma*, these barrens appear to be maintained by sea urchins at relatively low densities (<10 m^{-2}). Secondly, the *H. erythrogramma* barrens are a critical habitat for the introduced Asian kelp *Undaria pinnatifida* (Harvey) Suringar, an annual species which can form dense stands on *H. erythrogramma* barrens during the sporophyte growth season (Sanderson and Barrett 1989, Sanderson 1990, Sanderson 1997, Valentine and Johnson 2003, 2004, 2005).

Given the ecological implications of the presence of sea urchin barrens and their importance as a habitat for dense stands of *Undaria pinnatifida* sporophytes, they represent a serious issue for management of the coastal zone. Re-establishment of native canopy-forming species on urchin barren habitats will not only lead to higher productivity and biodiversity but it is also likely to result in the subsequent inhibition of development of *U. pinnatifida* sporophytes (Valentine and Johnson 2003, 2004). To determine whether management options exist to promote recovery of native canopy-forming species, it is vital to identify the factors responsible for persistence of the barren state.

Persistence of urchin barrens may not necessarily be dependent on continued grazing by sea urchins. We recently removed sea urchins from experimental plots on an urchin barren in Tasmania, and despite the lack of significant grazing saw no evidence of recovery of native canopy-forming algae after 30 months, even when combined with removal of *Undaria pinnatifida* sporophytes and addition of an enhanced supply of native algal spores (Valentine and Johnson 2005).

In this study, we extend our investigation of macroalgal recovery using transplant experiments. In order to settle propagules of native species on paving blocks, we deployed the blocks in a habitat dominated by native canopy-forming species. These paving blocks were subsequently transplanted to plots in an adjacent sea urchin/*Undaria pinnatifida*-dominated habitat, from which sea urchins were removed. Combined with appropriate handling controls, this approach allowed assessment of whether recovery of native canopy-forming algae on sea urchin barrens can be inhibited in the absence of intense sea urchin grazing.

Materials and methods

Study site

The experiment was conducted at 7–10 m depth on rocky reef at Lords Bluff, situated at the northern extremity of the Mercury Passage on the east coast of Tasmania (42°32′S, 147°59′E). At this site, a large *Heliocidaris erythrogramma* barren was found adjacent to reef dominated by a diverse assemblage of native canopy-forming species (hereafter termed 'algal bed') including the common kelp *Ecklonia radiata* (C. Agardh) J. Agardh and the fucoids *Phyllospora comosa* (Labillardière) C. Agardh, *Carpoglossum confluens* (R. Brown *ex* Turner) Kützing and *Seirococcus axillaris* (R. Brown *ex* Turner) Greville. While we have no quantitative data on the algal community prior to formation of the sea urchin barren, interviews with commercial divers operating in this area, and a clear negative relationship between native algal abundance and sea urchin density (Johnson et al. 2004) indicate that sea urchins are the primary cause of the loss of native canopy-forming algae from 'barren' rocky reefs. The sea urchin barren is colonised seasonally (in winter and spring) by dense stands of sporophytes of the introduced Asian kelp *Undaria pinnatifida*. The 'sea urchin barren' and 'algal bed' provide a basis for comparison in the experimental manipulations.

Experimental manipulations

Concrete paving blocks (29 cm×19 cm×9 cm) were used as settlement substrata, providing a horizontal area of 551 cm^2 on their top surface for algal recruitment. Concrete has been used previously in studies of algal succession and is suitable in mimicking natural reef surfaces (Foster 1975). Within each habitat, individual paving blocks were haphazardly deployed from the research vessel along approximately 100 m of coastline, at least 30 m away from the boundary between the algal bed and the urchin barren habitat, at a depth of 7–10 m. Following deployment, paving blocks were randomly assigned to experimental treatments using random number tables. The initial deployment occurred in August 2000 and there were ten replicate paving blocks in each treatment (see Figure 1).

Transplantation of paving blocks took place approximately three months after the initial deployment, while assessment of macroalgal abundance was carried out three, seven and 11 months after transplantation. During the transplant process, paving blocks were placed carefully into a large bin by divers, then slowly hauled to the surface. On the surface, paving blocks were placed in bins containing fresh seawater and immediately covered with hessian (=burlap) shade cloth to minimise exposure to direct sunlight. Paving blocks were transplanted within 45 min of reaching the surface. Ten replicate paving blocks were also deployed in each habitat at the time of transplantation (i.e., NT and BT) to assess algal recruitment after the time of transplant. The handling control treatment (NH) was included to investigate potential artefacts associated with the transplantation process. This involved lifting paving blocks from the algal bed and handling them in exactly the same way as transplanted paving blocks, before re-deploying them in the same area.

Sea urchin removal

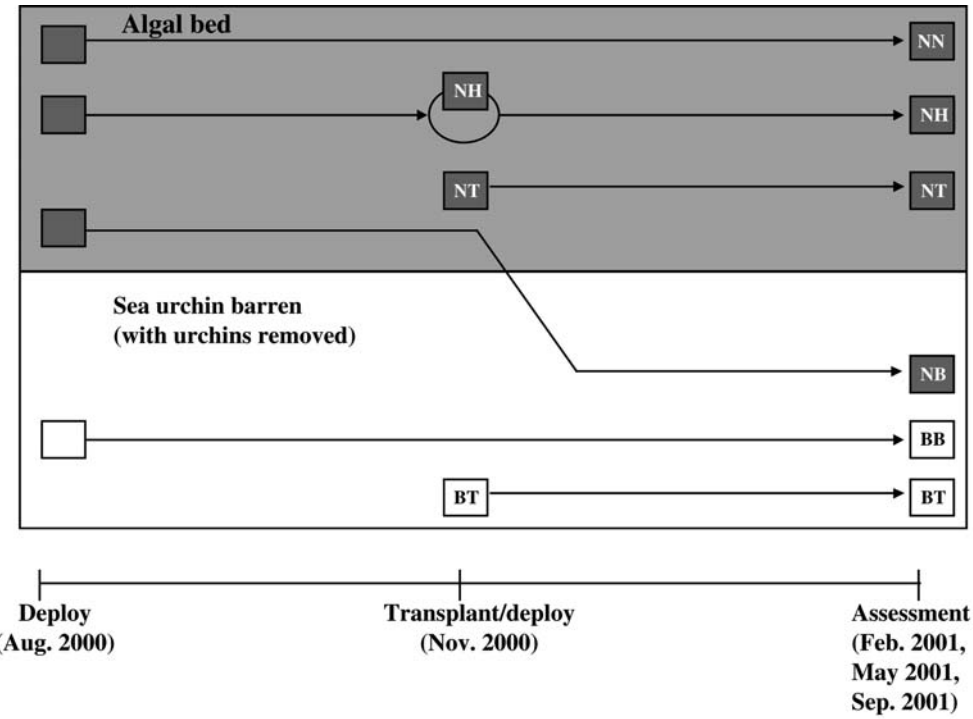
Paving blocks deployed or transplanted to the urchin barren were positioned in areas from which sea urchins were removed every 4–6 weeks (removal areas were 16 m^2 in area). This maintained an urchin density of <0.5 m^{-2} in removal areas compared to an average of 7.1 m^{-2} on an adjacent un-manipulated reef. An unexpected and brief intrusion of sea urchins into removal areas occurred in the barren zone during the summer period (January–April 2001), when densities temporarily attained ca. 5 m^{-2}. In the algal bed where sea urchins were not manipulated, densities averaged 2.7 m^{-2}.

Assessment of algal abundance

The percentage cover of algae, sessile invertebrates and sediment on paving blocks was estimated by recording taxa occurring under 50 regularly spaced intercepts of a point intercept quadrat. The quadrat covered the entire upper surface of the paving block and was positioned above the algae by a frame. Organisms were identified *in situ* to the highest taxonomic resolution possible. For canopy-forming algae, identification to species level was possible, however, it was necessary to allocate other species to functional groups (e.g., foliose red algae, brown turf algae). The density of recruits of canopy-forming species was also measured on each paving block by recording all recruits once they could be identified to species level. When recruitment was particularly dense, recruits were counted in each of four replicate 7 cm×7 cm quadrats randomly positioned on each paving block. At the conclusion of the experiment in September 2001 the depth of accumulated sediment on the paving blocks was measured to the nearest millimetre.

Analysis

The effect of the various 'treatments' on algal abundance was analysed using a one-way analysis of variance (ANOVA), with six levels of "treatment" (see Figure 1). Where appropriate, differences between treatments were investigated using the Ryan-Einot-Gabriel-Welsch (REGW) multiple range test. This analysis was conducted for data collected at the conclusion of the experiment in September 2001, 11 months after the transplantation. This allowed sufficient time for recruitment patterns of



TREATMENT	PURPOSE
NN	Assesses recruitment of macroalgae to paving blocks in the dense algal bed between August 2000 and the assessment dates in 2001.
NH	Handling control. Comparison with NN allows assessment of the effects of handling on macroalgal survival during the transplantation process.
NT	Assesses recruitment of macroalgae in the algal bed after the time of transplantation in November 2000.
NB	Assesses change in macroalgae following transplant from the algal bed to the urchin barren.
BB	Assesses recruitment of macroalgae to paving blocks on the urchin barren.
BT	Assesses recruitment of macroalgae on the urchin barren after transplantation.

Figure 1 Experimental design and transplant protocol.
Ten replicate paving blocks were deployed for each treatment.

macroalgae to be observed, as well as allowing enough time for development of *Undaria pinnatifida* sporophytes. Prior to all univariate tests, transformations to stabilise variances were determined from the relationship between group standard deviations and means (Draper and Smith 1981). Transformations are expressed in terms of the untransformed variate, Y. Univariate tests were undertaken using the SAS® (Cary, USA) statistical package.

The relationship between sediment abundance and algal cover on paving blocks was examined by plotting values of cover across all treatments against both sediment cover and an index of sediment load. This analysis also utilised data collected from additional paving blocks deployed as part of a broader experiment. The index of sediment load (SL) was defined as: SL=(% cover*depth)/100. Linear regression was used to investigate the relationship between sediment cover and foliose algal cover, while quantile regression was used to examine the upper bounds of the relationship between sediment load and foliose algal cover. Coefficients and confidence intervals for the quantile regression were estimated using the R statistical package (http://www.r-project.org/; version 2.0.1, 2004).

Results

Response of native canopy-forming algae to experimental manipulations

Native canopy-forming algae showed a clear response to experimental treatments (Figure 2b, Table 1). A range of macroalgae, including several native canopy-forming species, recruited successfully to paving blocks deployed in the algal bed (Figure 3). In contrast, native can-

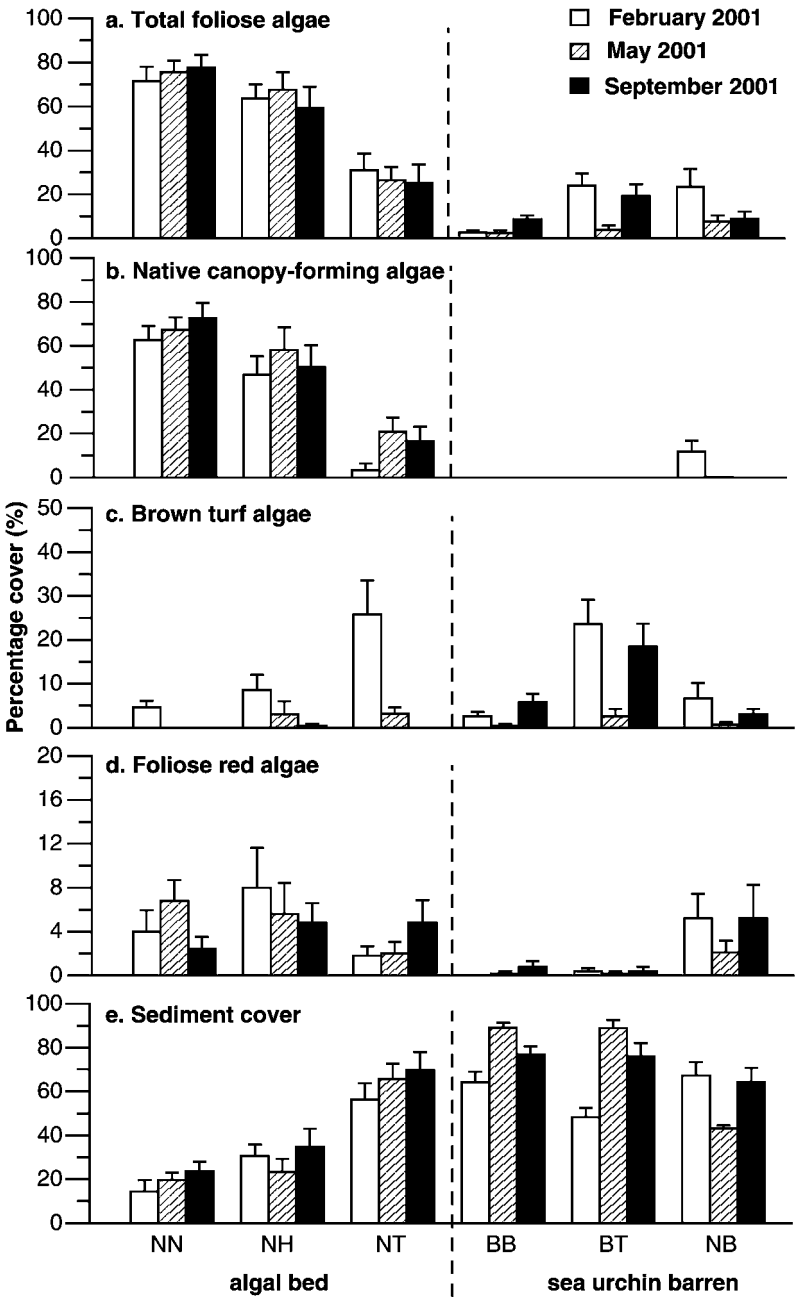


Figure 2 Response of algae and sediment to experimental manipulations.
Data are mean percentage cover (+SE) of ten replicate paving blocks per treatment. The dotted vertical line separates paving blocks present in the two habitats at the time(s) of assessment. For treatment codes refer to Figure 1.

opy-forming species did not recruit to paving blocks deployed in the sea urchin removal areas in nearby barren habitat (Figure 2b). While we did not assess algal abundance immediately prior to transplantation, high densities of brown algal recruits were observed on transplanted paving blocks. These recruits were generally <1 mm in length and were too small to identify to species level. Three months after the time of transplanting, average densities of native canopy-forming algal recruits (all species combined) on undisturbed (NN) paving blocks in the algal habitat exceeded 1.2×10^4 m^{-2}.

Transplantation of paving blocks from the algal bed to the barren habitat resulted in a dramatic reduction in cover of native canopy-forming species (Figure 2b). Three months after the time of transplanting, cover averaged 62.8%$\pm$6.3 SE on undisturbed (NN) paving blocks, compared with 11.8%$\pm$5.0 SE for transplanted (NB) paving blocks. Only a small proportion of native canopy-forming algal cover on undisturbed paving blocks could be attributed to recruitment after the time of transplant, since the NT treatment averaged only 3.4%$\pm$1.8 SE cover at the February 2001 assessment. In subsequent assessments, cover declined to undetectable levels on the transplanted paving blocks, while gradually increasing on control paving blocks in the algal bed. Development of macroalgae on paving blocks treated as handling controls was not significantly different from that on undisturbed paving blocks (NN) (Table 1).

The results also indicate that recruitment success for native canopy-forming species was dramatically lower in

Table 1 Results of one-way ANOVAs examining the effect of experimental manipulation on cover of algae and sediment, assessed in September 2001.

Functional form (transformation)	Df	MS	F	p	REGWQ tests
Total foliose algae (no transformation)	5, 54	8252.80	20.99	<**0.001**	NN NH NT BB BT NB
Native canopy-forming algae {log (y+0.1)}	5, 54	72.54	56.74	<**0.001**	NN NH NT BB BT NB
Ephemeral brown algae ($y^{0.33}$)	5, 54	5.16	14.61	<**0.001**	NN NT NH NB BB BT
Foliose red algae (sqrt)	5, 54	1.54	1.48	0.213	
Sediment cover (no transformation)	5, 54	1361.87	12.88	<**0.001**	NN NH NT BB BT NB
Sediment load (no transformation)	5, 54	19.70	6.43	<**0.001**	NN NH NT BB BT NB

Significant tests are shown in bold face. For REGWQ tests, a horizontal underline indicates treatments that are not significantly different from each other (α=0.05). Refer to Figure 1 for treatment codes.

the period following transplantation compared with the previous three months. Cover of native canopy-forming species on paving blocks deployed prior to transplant (i.e., NN treatment) averaged 67.2%±5.7 SE following 11 months of submergence in May 2001 (Figure 2b). In contrast, cover of native species on paving blocks deployed after transplant (NT treatment) averaged only 16.6%±6.7 SE during the September 2001 assessment, despite being submerged for an equivalent 11 month period (Figure 2b).

Response of understorey species

The brown turf functional group, comprising a range of ephemerals including *Asperococcus* spp., *Colpomenia* spp., *Scytosiphon* spp. and several other unidentified species was generally low in cover for most treatments, usually averaging <10% (Figure 2c). There were, however, some notable exceptions. At the February 2001 assessment, in both habitat types more filamentous brown turfing algae developed on paving blocks dep-

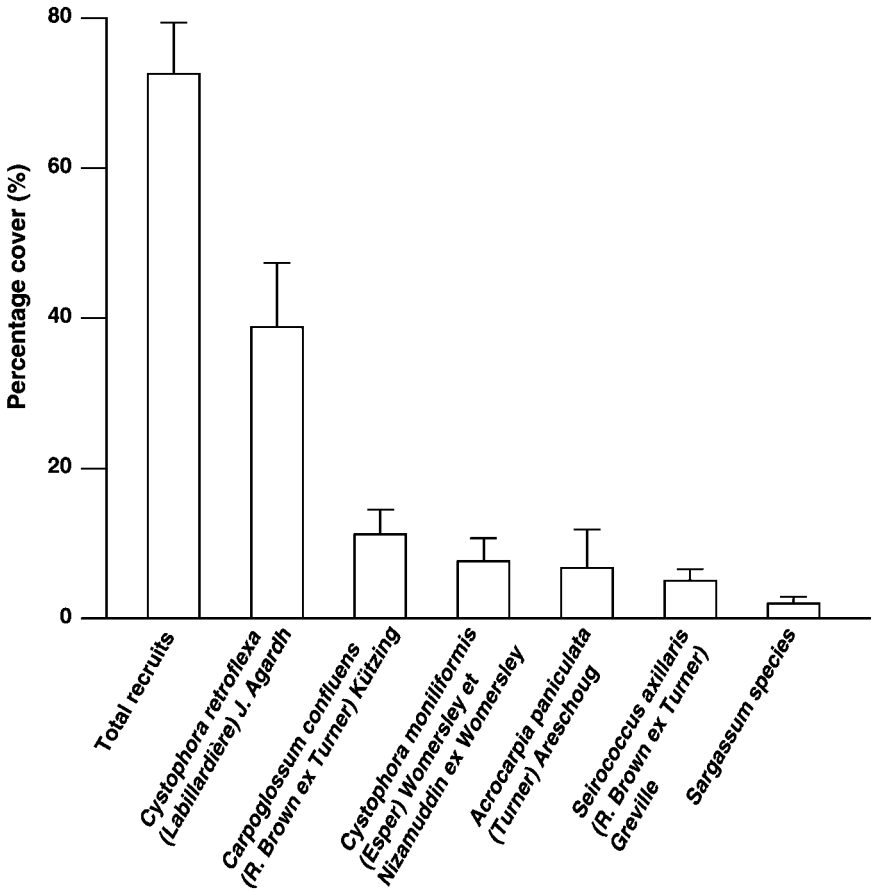


Figure 3 Relative abundance of native native canopy-forming algae occurring on undisturbed (i.e., NN) paving blocks deployed in the native zone, assessed in September 2001.
Data are mean percentage cover (+SE) of ten replicate paving blocks.

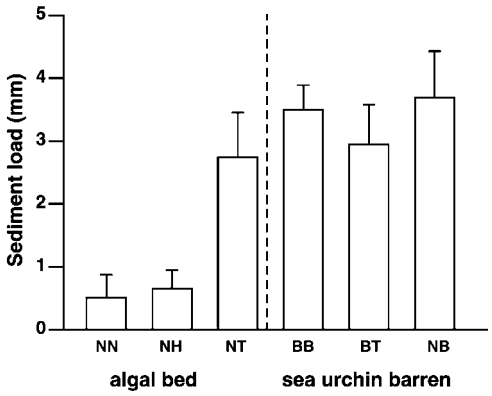


Figure 4 Effect of experimental manipulations on sediment accumulation following September 2001 assessment.
Data represent mean sediment loads (+SE) of ten replicate paving blocks per treatment. Sediment load (SL) is an index of sediment accumulation and is calculated SL=(% cover×depth)/100. The dotted vertical line separates paving blocks present in the two habitats at the time of assessment. For treatment codes refer to Figure 1.

loyed at the time of transplant (NT and BT) than on those established at the beginning of the experiment (i.e., NB and NN), indicating opportunistic colonisation of newly available substratum. Cover declined in both NT and BT treatments by the May assessment, before increasing again on those paving blocks on the barren (BT) but not in the algal bed (NT). At the conclusion of the experiment, cover of ephemeral brown algae was higher in the BT treatment than in all other treatments (Figure 2c, Table 1).

Cover of foliose red algae was also very low across all treatments, averaging <5% (Figure 2d). Although cover of foliose red algae was generally higher on paving blocks deployed in the algal bed than on those deployed on the urchin barren, these differences were not significant at the completion of the experimental period (Table 1).

Patterns of sediment abundance

Paving blocks in the various treatments accumulated different amounts of sediment (Figure 2e, Table 1). The undisturbed paving blocks (NN) and handling controls (NH), the only two treatments to be located in the algal bed throughout the experiment, recorded dramatically lower sediment cover compared to all other treatments over the entire period of the experiment. This trend was also reflected in the estimates of sediment load collected at the end of the experiment in September 2001 (Figure 4, Table 1).

Transplantation of paving blocks from the algal bed to the barren habitat (NB) resulted in a significant increase in sediment cover that persisted throughout the experimental period (Figure 2e, Table 1). Although we did not assess paving blocks quantitatively prior to transplantation, we noted that paving blocks from the initial deployment in the algal bed had low cover and depth of sediment, while at this time paving blocks on the barren habitat demonstrated a high cover and depth (up to 10 mm) of sediment. After transplanting paving blocks from the algal bed to the barren habitat, sediment up to 10 mm in depth accumulated on transplanted paving blocks within two weeks of transplantation.

The pattern of sediment cover was generally the converse of that observed for native canopy-forming algae. When cover of native canopy-forming algae was high, cover of sediment was low and vice-versa. We examined this trend in more detail by plotting values of sediment cover against total foliose algal cover, across all treatments (note that NT and BT treatments were excluded from this analysis because they were deployed part way through the experiment). This analysis revealed a significant negative relationship between the cover of sediment and total foliose algal cover (Figure 5). Although sediment cover provided some useful patterns to explore in relation to algal abundance, a better indicator of the amount of sediment on the paving blocks is given by the index of sediment load which includes components of both sediment depth and cover (see Materials and methods).

The relationship between algal cover and sediment load (Figure 6) was different from that between algal cover and sediment cover (Figure 5). While cover of foliose algae varied substantially under conditions of low sediment load, high cover of foliose algae only occurred when sediment load was low. Under conditions of high sediment load, only low cover of foliose algae developed. It should also be highlighted that while, in general, sediment load was higher on paving blocks either deployed or transplanted to the urchin barren compared with those in the algal bed, there were examples of high sediment load occurring on particular paving blocks in the algal bed (Figure 6).

Discussion

There are many examples of experiments on sea urchin barrens that demonstrate re-establishment of native canopy-forming algae in plots from which sea urchins are removed (Duggins 1980, Chapman 1981, Himmelman et al. 1983, Keats et al. 1990, Leinaas and Christie 1996, Agatsuma et al. 1997, Shears and Babcock 2002). In marked contrast, the results of our experiments showed poor recruitment of native canopy-forming species on paving blocks in the barren habitat and a marked reduction in cover of native canopy-forming algal recruits transplanted to barrens in the absence of high densities of sea urchins.

While it is possible that the brief incursion of sea urchins into the urchin-removal areas may have compromised the experiment, we believe that it is unlikely to account for the poor recovery of native canopy-forming species, for two main reasons. Firstly, while we regularly observed *Heliocidaris erythrogramma* feeding during our frequent dives on the urchin barren (predominately on drift algae), we never observed sea urchins grazing the horizontal surface of the paving blocks. Secondly, the decline of native canopy-forming algal recruits that was observed on transplanted paving blocks was clearly evident before the sea urchin intrusion occurred. For these reasons we suggest that other mechanisms may operate

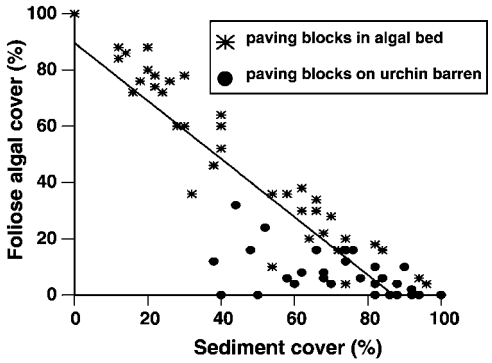


Figure 5 Relationship between sediment cover and total cover of foliose algae on paving blocks, assessed in September 2001. Paving blocks in each habitat include transplanted paving blocks. Regression equation: $y=-1.031x+89.62$, $n=70$, $r^2=0.79$, $p<0.0001$.

to prevent recovery of native macroalgae on these sea urchin barrens.

Decline of algal recruits transplanted to sea urchin barrens

If sea urchins were not the primary cause of the decline in canopy species transplanted to sea urchin barrens then what other mechanisms are important? While the presence of turfing algae has been demonstrated to prevent re-establishment of large brown macroalgae (Dayton et al. 1984, Kennelly 1987), only low cover of foliose red and brown turfing algae was recorded on paving blocks transplanted to and deployed on the urchin barren and is unlikely to account for inhibition of native canopy species. We can also discount the potential inhibitory effects of a dense canopy of *Undaria pinnatifida* sporophytes on native algal abundance. In the 2001 sporophyte growth season *U. pinnatifida* sporophytes developed at low densities in our study area (Valentine and Johnson 2005) so that *U. pinnatifida* cover was negligible, both on the paving blocks themselves and in the immediate area surrounding them. This is also consistent with our previous work demonstrating that removal of the *U. pinnatifida* canopy on the urchin barren did not significantly affect cover of native foliose algae, even in the absence of sea urchins (Valentine and Johnson 2005).

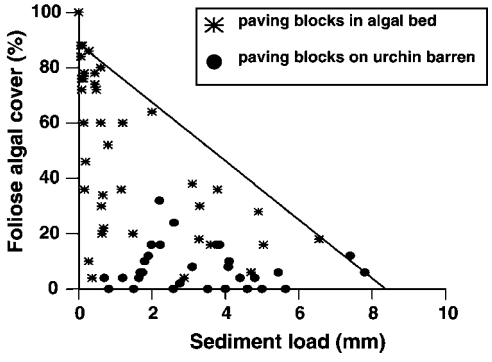


Figure 6 Upper bounds of the relationship between sediment load and foliose algal cover on paving blocks, assessed in September 2001.
The line represents a linear regression on the 90th quantile. Confidence intervals (70%) were plotted but could not be distinguished from the regression line. Sediment load (SL) is an index of sediment accumulation and is calculated SL=(% cover×depth)/100. Paving blocks in each habitat include transplanted paving blocks. Quantile regression equation: $y=-10.594x+88.636$, $n=70$, $p<0.0001$.

Although the handling process itself did not result in a significant decline in native canopy-forming algae, the change in light environment associated with transplantation from the algal bed to the barren might have contributed to mortality of macroalgal recruits. Many paving blocks deployed in the algal bed were subject to shading by native canopy-forming algae and would have experienced increased light levels following transplantation, potentially leading to photoinhibition of algal recruits (e.g., Hanelt 1996, Hanelt et al. 1997). There were also other paving blocks in the algal bed, however, that were not subject to shading by canopy species and would not have experienced a dramatic change in light environment after transplant. If the altered light environment contributed to algal mortality we would not have recorded mortality across all paving blocks. Consequently, we suggest that a change in light environment is unlikely to account for the observed patterns of algal mortality.

The effects of sediment accumulation on settlement paving blocks in the barren habitat appears the most likely explanation for the observed inhibition of native canopy-forming algal recruits. Previous studies have demonstrated the inhibitory effects of sediment on rocky reef organisms (reviewed by Airoldi 2003). It seems likely that rapid accumulation of sediments on paving blocks transplanted to the barren zone would have at least resulted in partial burial, with concomitant effects in reducing irradiance and photosynthetic rates of recruits. Additional negative effects of sediment on early developmental stages of macroalgae include the combined effects of water motion and sediment scouring the substratum (Coelho et al. 2000), and the toxic effects of hydrogen sulphide associated with marine sediments (e.g., Chapman and Fletcher 2002).

Lack of recruitment to paving blocks on urchin barren

The lack of recruitment of native canopy-forming species on paving blocks deployed on the urchin barren is also likely to have been related to sediment accumulation. In addition to the detrimental effects of sediment burial and scour on macroalgal propagules, recruitment of canopy-forming species would be limited by the replacement of stable hard substrata with unstable sediment particles (Airoldi 2003). Laboratory experiments conducted with *Macrocystis pyrifera* (Linnaeus) C. Agardh have demonstrated that effective recruitment can be reduced by spores attaching to sediment grains, which are subsequently washed away from the benthos by waves and water motion (Devinny and Volse 1978). Similarly, experiments have demonstrated that the presence of sediment particles inhibited insertion, germination, survival and maturation of gametophytes of *Undaria pinnatifida* and *Ecklonia cava* Kjellman (Arakawa and Matsuike 1992).

Another possible reason for the lack of recruitment on the urchin barren relates to supply of algal propagules. Since dispersal of large brown algae is generally thought to be limited, with most recruits occurring within a few metres of the parent plants (Anderson and North 1966, Ambrose and Nelson 1982, Dayton 1985, Andrew and Viejo 1998), recovery of native canopy-forming species may be restricted by their poor dispersal characteristics. This is unlikely to account for the lack of recruitment observed in this study, since dispersal via spores should have occurred from nearby plants in shallower water at the study site where a dense cover of native species was evident. Dispersal from a shallow algal fringe where macroalgae have refuge from sea urchin grazing has been attributed to the rapid recovery of kelp beds on barren grounds in the northwestern Atlantic Ocean following mortality of sea urchins (Scheibling 1986, Johnson and Mann 1988, 1993).

Patterns of sediment accumulation

While high sediment loads developed on some paving blocks in the native algal bed, it is clear that, on average, sediment loads were notably higher on the urchin barren than on the substratum beneath dense macroalgal cover. This observation is consistent with our observations from other experiments showing an immediate and significant increase in sediment cover following artificial removal of the canopy (Valentine and Johnson 2003) and following natural canopy dieback (Valentine and Johnson 2004). Indeed, high cover of sediment is a prominent feature of *Heliocidaris erythrogramma* barrens in this region (Johnson et al. 2004).

Why does reduced canopy cover result in increased sediment accumulation on rocky reefs? There are several possible explanations. The most compelling is that sweeping of the seafloor by macroalgal fronds in dense beds prevents accumulation on exposed horizontal surfaces of reef (e.g., Kennelly 1989). While it is possible that rates of sediment deposition were locally greater on the barren habitat than in the algal bed, reflecting small-scale variability in sediment deposition (Airoldi and Virigilo 1998), it seems unlikely that the negative relationship between sediment cover and algal cover is coincidental. We did not quantify spatial variability in sedimentation and further research should address both the rates of sediment deposition and accumulation at a range of spatial and temporal scales.

Although our data show a clear negative relationship between sediment load and foliose algal cover, the relationship is correlative and does not infer causality. Further experiments are required to determine whether sediment controls algal abundance, whether algal abundance controls sediment accumulation, or whether a combination of both mechanisms operate. While our data are correlative, we argue that the combined evidence indicates that sediment is an important factor shaping macroalgal community structure. Our canopy removal experiments showing an increase in sediment cover on the reef surface relative to areas where the canopy was left intact (Valentine and Johnson 2003) and identical observations following a natural canopy dieback (Valentine and Johnson 2004), clearly indicates that the presence of a canopy inhibits sediment accumulation, as has been demonstrated elsewhere (Kennelly 1987, Kennelly and Underwood 1993, Melville and Connell 2001). In separate experiments we also measured cover of the sediment matrix on the urchin barren habitat and it was consistently high (average $>50\%$) over a 30-month period (Valentine and Johnson 2005).

It should also be emphasised that while the exotic kelp *Undaria pinnatifida* was not abundant on the urchin barren during the present study, this alga occurred abundantly in this habitat in previous years (Valentine and Johnson 2005). A possibility is that *U. pinnatifida* can tolerate a degree of sediment stress and may be less sensitive to the negative effects of sediment compared with native canopy-forming species. Alternatively, the opportunistic nature of *U. pinnatifida* may enable it to colonise urchin barrens during temporary 'recruitment windows' provided by sediment removal associated with storms (e.g., Littler et al. 1983, Renaud et al. 1997). The potential interaction between sediment dynamics and *U. pinnatifida* warrants further research.

Our overall conclusion is that, in this system, sediment accumulation appears to act as a positive feedback mechanism to maintain barren habitat once it is formed, by inhibiting the early developmental stages of native canopy-forming algae. This indirect link between sea urchins and sediment levels, whereby sea urchins mediate sediment dynamics through their grazing activities on kelp plants, has been suggested previously (Estes and Palmisano 1974). Identifying the source of accumulated sediment is potentially an important management issue. While sedimentation is a natural process on rocky reefs, various anthropogenic activities such as deforestation, dredging, industrial and domestic discharges, construction activities and land reclamation can lead to increased sedimentation rates (Airoldi 2003). A critical question is whether sediment accumulating in our study area is influenced by human activities. If sediment deposition can be linked to human activity, then recovery of native species may require management to control sedimentation. If the sediments at this site are derived from natural sources, then recovery of native canopy species is problematic since removal of both sea urchins and *Undaria pinnatifida* from these *Heliocidaris erythrogramma* barrens is insufficient to promote regrowth of native canopy-species (Valentine and Johnson 2005). Clearly, preventing destructive grazing of native canopy-forming species in the first place is the preferred management option.

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