

# Small-scale variability in the dispersion of the sea urchin *Heliocidaris erythrogramma* among boulders

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**ABSTRACT:** Densities of many organisms, particularly invertebrates, are inherently patchy from place to place, with much variability at small spatial scales. Intertidal and shallow subtidal boulder fields in New South Wales, Australia, support a diverse suite of species, many of which have very patchy distributions among boulders. In this study, the purple urchin *Heliocidaris erythrogramma* was very patchily distributed at small spatial scales, being abundant under some boulders and absent from others. This pattern was found consistently at different times and in boulder fields tens of kilometres apart. Experiments were done to identify mechanism(s) that may establish and maintain the observed distribution. Small-scale variability in distribution was established early in the animals' life-cycle, because *Heliocidaris* recruits were more abundant on boulders with adult urchins than on boulders without adult urchins. Manipulative experiments indicated that the pattern of dispersion was also maintained by the behavioural responses of juvenile and adult urchins to either feature(s) of boulders or to cues associated with conspecifics. When *Heliocidaris* were transplanted to boulders originally without urchins, they left at a greater rate than did urchins on boulders that originally had urchins but from which urchins had been removed. In addition, juvenile and adult urchins colonised more boulders with urchins than boulders without urchins. Behavioural responses to unidentified but specific requirements of habitat provided by some boulders may thus be important in maintaining non-random densities of urchins among boulders.

**KEY WORDS:** Boulder field · Sea urchin · *Heliocidaris* · Small-scale · Movement · Recruitment · Dispersion · Subtidal · Intertidal

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## INTRODUCTION

Spatial and temporal patchiness is an inherent feature of assemblages in freshwater, terrestrial and marine environments (Wiens et al. 1993, Underwood & Chapman 1996, Downes et al. 2000a). In recent years, several studies have emphasised that variation in the distribution and abundance of organisms does not occur at a single scale, but rather at a hierarchy of different spatial scales (e.g. Morrisey et al. 1992, Beisel et al. 1998). Moreover, a large amount of variation in abundances of species occurs at very small spatial scales (Underwood & Chapman 1996, Archambault & Bourget 1996).

In the past, variability in the abundance of intertidal organisms was thought to be governed primarily by

broad environmental gradients, such as height above sea-level or exposure to wave-action (Connell 1972). It has since become apparent that physical stresses associated with broad environmental gradients cannot, on their own, describe patterns of abundance of many intertidal organisms (Underwood 1984, Benedetti-Cecchi 2000). Thus, intertidal ecologists are increasingly recognising the importance of the complex interaction of large-scale factors with local, small-scale processes in regulating intertidal assemblages (Menge & Olson 1990).

Small-scale environmental variation is a feature of many habitats, such as rocky shores (e.g. Paine & Levin 1981) and can lead to a complex array of microhabitats within an area of a few metres. Microhabitats often influence small-scale patterns of distribution and abun-

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dance of organisms, as many species are aggregated in some microhabitats and absent from others. Organisms may respond to physical features of habitat, e.g. topographic complexity (Raffaelli & Hughes 1978, Moran 1985), and/or to biogenic structures, e.g. sessile organisms such as algae (Worthington & Fairweather 1989).

Causes of variable dispersion of organisms may be categorised into 3 broad classes of models: patterns of birth/immigration, differential rates of emigration or mortality, or behavioural responses to habitat or conspecifics within a patch (e.g. Underwood & Denley 1984). These models may act independently or in combination to explain the pattern under investigation. Spatial and temporal variability in settlement of marine invertebrates can be important in regulating recruitment and can vary at a range of scales, from metres to hundreds of kilometres (Balch & Scheibling 2000, Jenkins et al. 2000) and from days to years (Loosanoff 1964, Jenkins et al. 2000). Recruitment is the result of processes affecting settlement, coupled with early post-settlement mortality (for review see Hunt & Scheibling 1997) and/or migration of juveniles that occurs prior to the first census (Keough & Downes 1982). Due to the inherent difficulty associated with obtaining an accurate measure of settlement and the need to sample at frequent intervals to avoid confounding patterns of settlement from patterns affected by early post-settlement processes (Keough & Downes 1982), most studies have measured patterns of recruitment rather than patterns of settlement. After settlement, patterns can be modified by subsequent mortality of adults (e.g. Connell 1961), or mobile animals may move to establish associations with particular microhabitats (e.g. Crowe 1996).

Distributions and abundances of organisms living in boulder fields are extremely variable at small spatial scales, because many species found under boulders are not often found in adjacent habitats and/or because many are extremely aggregated (Smith & Otway 1997, Chapman 2002a,b, Grayson & Chapman 2004). These species are often extremely patchy at a hierarchy of spatial scales, from among different boulder fields to among individual boulders, with most variation at the scale of individual boulders within a site (Smith & Otway 1997, Chapman 2002a, 2005, Grayson & Chapman 2004).

Relatively little is known about the ecology and distribution of sea urchins inhabiting boulder fields, even though they are a conspicuous and abundant member of benthic marine assemblages and their ecological importance has been documented in different habitats (e.g. Benedetti-Cecchi & Cinelli 1995) and in many geographical locations (e.g. Andrew & Underwood 1989, Bulleri et al. 1999). We evaluated the model that the sea urchin *Heliocidaris erythrogramma* (hereafter

*Heliocidaris*) has an aggregated distribution under boulders. Most studies on the dispersion of mobile organisms in boulder fields have been about molluscs (Smith & Otway 1997, Chapman 2002a,b, 2005, Grayson & Chapman 2004), although Chapman (2002a) found that the sea star *Patiriella exigua* was very patchily distributed among boulders. In addition, we used manipulative field experiments to examine models that may explain the dispersion of *Heliocidaris*, specifically investigating: (1) patterns of recruitment and (2) behavioural responses of post-recruit urchins to different types of boulders.

## MATERIALS AND METHODS

This study was conducted in 3 intertidal to shallow subtidal boulder fields in New South Wales, Australia: the Cape Banks Scientific Marine Research Area (hereafter referred to as Cape Banks), Clovelly Bay and Long Reef Aquatic Reserve (hereafter referred to as Long Reef; Fig. 1). The boulder field at Cape Banks is sheltered from direct wave-action except during rough seas and has been described previously by Chapman & Underwood (1996) and Grayson & Chapman (2004). The area used in this study was similar to that described in Chapman & Underwood (1996) and Grayson & Chapman (2004). The boulder field at Clovelly Bay is sheltered from direct wave-action, except during rough seas. The boulders are composed mostly of sandstone and, like those at Cape Banks, rest on bedrock, overlaid by shell grit, sand or small patches of algal turf (Grayson & Chapman 2004). The headland of Long Reef is surrounded by an extensive rock platform with small, sandy beaches and boulder fields (Smith & Otway 1997, Chapman 2005). Sampling was done in the boulder field on the south-east corner of the rock platform where the boulders are moderately exposed to the dominant south-easterly swell (as in Chapman 2005). The boulders are composed predominately of shale and rest on similar substratum to that at Cape Banks and Clovelly Bay.

At Cape Banks in February 2003, 20 haphazardly chosen boulders were lifted vertically or overturned (depending on their size and the surrounding area), and all *Heliocidaris* visible on the undersurface of or below each boulder were counted. The upper size limit was a boulder that could be replaced in its original position without extreme disturbance and dislodgment (Chapman & Underwood 1996).

To evaluate the generality of patterns found at Cape Banks, boulder fields at Clovelly Bay and Long Reef were sampled similarly in February and July 2003, respectively, although the number of boulders sampled was increased to 30. To evaluate the temporal ge-

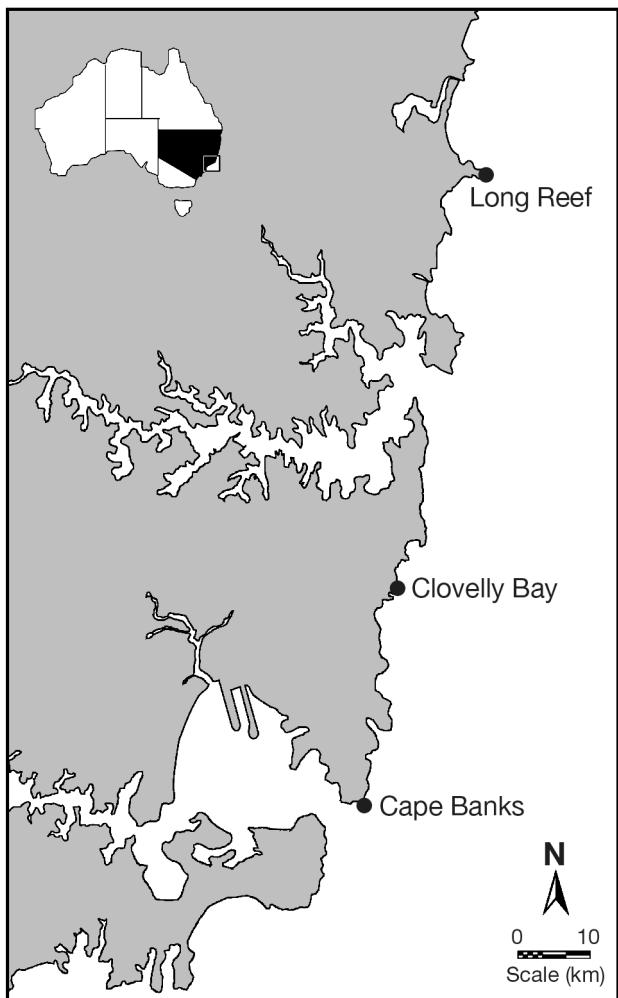


Fig. 1. Study sites on the coast of New South Wales, Australia

nerality of these patterns, the boulder fields at Cape Banks and Clovelly Bay were re-sampled 1 mo (March) and 5 mo (July) after the initial sampling, using similar methods and  $n = 30$ .

Analyses showed that *Heliocidaris* were significantly aggregated under few of the available boulders (see Results). To evaluate the model that patterns of recruitment maintain this pattern, 2 hypotheses were tested. The first was that *Heliocidaris* will recruit in greater numbers to boulders already occupied by adult and juvenile *Heliocidaris* than to boulders without urchins. Second, new recruits will arrive on a greater proportion of those boulders that have adult and/or juvenile urchins than is the case for boulders without urchins. Recruits of *Heliocidaris* were defined as  $<1.5$  cm in test diameter, as this was the size at which individuals could be first observed without destructive sampling of the boulders. It therefore encompasses patterns of settlement and early mortality and/or

movement (Keough & Downes 1982). To test these hypotheses, 30 boulders with urchins (test diameter  $> 1.5$  cm) and 30 boulders without urchins of this size were haphazardly chosen from available boulders in Clovelly Bay and Long Reef. The undersurface of each boulder was searched exhaustively for *Heliocidaris*  $<1.5$  cm test diameter in June and July 2003 at Clovelly Bay and in July at Long Reef.

To evaluate the models that the above patterns may be established and/or maintained by juvenile and adult *Heliocidaris* (i.e.  $>1.5$  cm test diameter) moving among boulders in response to: (1) features of the boulders, (2) cues associated with conspecifics or (3) some combination of the two, hypotheses about the rates of colonisation and dispersal of adult *Heliocidaris* to and from the 2 types of boulders (boulders originally with urchins and boulders originally without urchins) were tested (Table 1). The above factors have the potential to affect the number of *Heliocidaris* per boulder and the number of boulders that are occupied by *Heliocidaris* within the boulder field. Model 1 predicts that if *Heliocidaris* respond to features of boulders, then: ( $H_1$ ) more *Heliocidaris* will colonise boulders from which *Heliocidaris* are removed (+UB – U) than boulders originally without urchins (–UB). It also predicts ( $H_2$ ) that a greater proportion of boulders from which *Heliocidaris* have been removed (+UB – U) will be re-occupied by *Heliocidaris* than will boulders originally without urchins (–UB). Furthermore, ( $H_3$ ) if *Heliocidaris* are transplanted from boulders with urchins to boulders without urchins, they will leave at a faster rate than they leave boulders originally occupied by urchins. Similarly, ( $H_4$ ) proportionally more unoccupied boulders (–UB) to which *Heliocidaris* have been experimentally added will lose urchins than will boulders originally occupied by adult urchins (+UB).

Alternatively, if only the presence of conspecifics influences the observed pattern, then ( $H_5$ ) if *Heliocidaris* are removed from boulders originally with urchins (+UB – U) and boulders originally without urchins (–UB) are left undisturbed, *Heliocidaris* will not colonise either type of boulder. In addition, ( $H_6$ ) if *Heliocidaris* are transplanted to unoccupied boulders, they will leave these boulders (–UB + U) at the same rate as they leave boulders originally occupied by adults, but from which other urchins are removed (+UB – U). Similarly, ( $H_7$ ) there will be no difference between the proportions of boulders that lose urchins irrespective of whether they were originally occupied by urchins. To test these hypotheses, we used the following treatments: (1) boulders originally with urchins (+UB), (2) boulders originally with urchins but from which urchins had been experimentally removed (+UB – U), (3) boulders originally without urchins (–UB) and (4) boulders originally without urchins but to which urchins

Table 1. *Heliocidaris erythrogramma*. Summary of models and hypotheses required to test the hypotheses about (a) colonisation and (b) dispersal to and from different types of boulders

Model	Hypotheses
1. <i>Heliocidaris</i> are found on a subset of available boulders because they respond to features of boulders	(a) Colonisation <b>H<sub>1</sub>:</b> <i>Heliocidaris</i> will arrive at a greater rate to boulders from which existing adult urchins have been experimentally removed (+UB – U) than to boulders not originally occupied by adult urchins (–UB) <b>H<sub>2</sub>:</b> Proportion of boulders to which urchins colonise will be greater for boulders from which urchins have been removed (+UB – U) than for boulders that had no urchins (–UB) (b) Dispersal When urchins are added to boulders <b>H<sub>3</sub>:</b> <i>Heliocidaris</i> will leave boulders not originally occupied by adult urchins (–UB + U) faster than they leave boulders originally occupied by adult urchins (+UB) <b>H<sub>4</sub>:</b> Proportionally more unoccupied boulders (–UB + U) will lose urchins than will boulders originally occupied by adult urchins (+UB)
2. <i>Heliocidaris</i> are found on a subset of available boulders because they respond to cues associated with the presence of or previous occupation by conspecifics	(a) Colonisation <b>H<sub>5</sub>:</b> There will be no colonisation of <i>Heliocidaris</i> to boulders from which existing adult urchins have been experimentally removed (+UB – U) and boulders not originally occupied by adult urchins (–UB) (b) Dispersal When urchins are added to boulders <b>H<sub>6</sub>:</b> There will be no difference in the rate at which <i>Heliocidaris</i> leave boulders not originally occupied by adult urchins (–UB + U) and boulders originally occupied by adults (+UB) <b>H<sub>7</sub>:</b> There will be no difference in the proportions of boulders that lose urchins between boulders that originally had adult urchins (+UB) and unoccupied boulders (–UB + U)

were experimentally added (–UB + U) (Table 2). Moreover, to differentiate between those urchins that colonise boulders from those individuals originally left on boulders, urchins required tags. Due to excessive disturbance associated with tagging individuals and leaving boulders overturned or repeatedly overturning them (Chapman & Underwood 1996) while urchins were being tagged (A. F. Smoothery unpubl. data), this procedure was not incorporated in the present study. All urchins used in the experiments were carefully removed from the boulder by hand to minimise injury to the animals and disturbance to the substrata under the boulder. Urchins were held in place on the undersurface of their respective boulder, and all urchins re-attached themselves within 2 min. Experimental manipulations were completed on 1 d.

The experiments were started at Clovelly Bay on 13 June 2003. Preliminary sampling showed that *Heliocidaris* colonised and dispersed from boulders after just 1 d. The boulders in this study were therefore sampled, and the number of *Heliocidaris* under each

boulder was recorded 1 d, 7 d and 14 d after the start of the experiment. Times of sampling were not independent because the same boulders were sampled each time.

To evaluate the temporal generality of these experiments, they were repeated on 12 July 2003 at Clovelly

Table 2. *Heliocidaris erythrogramma*. Treatments used to test the hypotheses about colonisation and dispersal to and from different types of boulders, and to test for experimental artefacts associated with transplanting to boulders originally without urchins (–UB + U). +UB – U: removal of *Heliocidaris* from boulders with urchins; –UB: unmanipulated boulders originally without urchins; –UB + U: *Heliocidaris* transplanted to boulders originally without urchins; +UB + U: *Heliocidaris* translocated from boulders with urchins to unfamiliar boulders with urchins; +UBD: disturbed *Heliocidaris* under boulders with urchins; +UB: unmanipulated *Heliocidaris* under boulders with urchins; ✓: treatment used; ✗: treatment not used

Procedure	— Colonisation —			Dispersal		
	+UB – U	–UB	–UB + U	+UB + U	+UBD	+UB
Disturbed	✗	✗	✓	✓	✓	✗
Moved to an unfamiliar boulder with urchins	✗	✗	✓	✓	✗	✗
Moved to a boulder without urchins	✗	✗	✓	✗	✗	✗
Removed from boulders with urchins	✓	✗	✗	✗	✗	✗

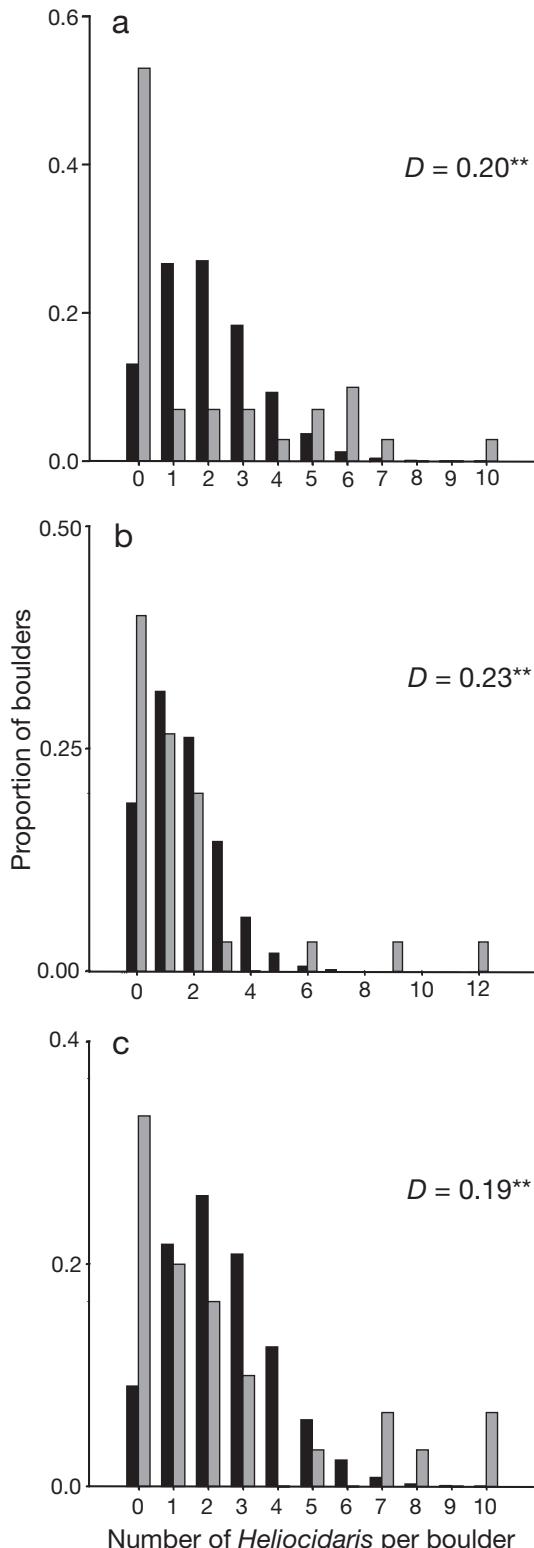


Fig. 2. *Heliocidaris erythrogramma*. Observed distribution (grey bars) of boulders and the expected (Poisson) distribution (black bars) for (a) Cape Banks, (b) Clovelly Bay and (c) Long Reef;  $n = 30$  boulders.  $D$  is the test statistic for Kolmogorov-Smirnov tests. \*\*Distributions were significantly different at  $p < 0.01$ .

Bay, although the number of boulders per treatment was increased to 15 to increase the power of the experiment. Due to the limited number of boulders with urchins, previously tagged boulders that did not have their density manipulated were re-used, although they were randomly allocated to new treatments. This minimised the possibility of confounding the past history with the effect of the treatment. The experiment was also done at Long Reef on 30 July 2003. Prior to starting the experiment, 15 boulders with urchins and 15 boulders without urchins were tagged. Due to the limited number of boulders without urchins, hypotheses about the dispersal of urchins from the 2 types of boulders were not tested at Long Reef.

## RESULTS

In each boulder field and at each time of sampling, *Heliocidaris* were not randomly distributed among boulders, but aggregated under some boulders and were absent from others (Fig. 2). Compared to a Poisson distribution, there were more boulders with no *Heliocidaris* and more boulders with relatively large numbers of *Heliocidaris* than expected (Kolmogorov-Smirnov tests,  $p < 0.01$ ).

### Processes that may act to establish and/or maintain the observed pattern

#### Recruitment

There were significantly more recruits of *Heliocidaris* on boulders with urchins with test diameter  $>1.5$  cm (+UB) than on boulders without urchins of this size (-UB), in each boulder field and at each time of sampling. Mean (+SE;  $n = 30$  boulders) numbers of recruits were: Clovelly Bay, 10 June 2003: +UB 1.20 (0.28), -UB 0.27 (0.13),  $t = 0.002$ ,  $p < 0.01$ ; 8 July 2003: +UB 1.43 (0.21), -UB 0.47 (0.16),  $t = 0.003$ ,  $p < 0.01$ ; Long Reef, 9 July 2003: +UB 1.03 (0.34), -UB 0.23 (0.10),  $t = 0.01$ ,  $p < 0.05$ .

Furthermore, during each time of sampling and in each boulder field, the proportion of boulders with urchins (+UB) that were colonised by recruits of *Heliocidaris* ( $<1.5$  cm) was significantly greater than the proportion of boulders without urchins (-UB) colonised by recruits (Clovelly Bay, 10 June 2003: proportion of  $n = 30$  +UB with recruits = 0.63, proportion of  $n = 30$  -UB with recruits = 0.16,  $\chi^2_1 = 13.61$ ,  $p < 0.001$ ; 8 July 2003: proportion of  $n = 30$  +UB with recruits = 0.57, proportion of  $n = 30$  -UB with recruits = 0.30,  $\chi^2_1 = 20.40$ ,  $p < 0.001$ ; Long Reef, 9 July 2003: proportion of  $n = 30$  +UB with recruits = 0.47, proportion of  $n = 30$  -UB with

recruits = 0.17,  $\chi^2_1 = 25.75$ ,  $p < 0.001$ ). Nevertheless, urchins did recruit to boulders that did not have adult urchins at the start of the experiment.

#### Behavioural responses of juvenile and adult *Heliocidaris*

On each day of sampling (1, 7 and 14 d after the experimental manipulation) at Clovelly Bay, the mean number of juvenile and adult *Heliocidaris* that colonised boulders from which urchins had been removed (+UB – U) was significantly greater than the number that colonised boulders without urchins (–UB; Fig. 3, Table 3a). When the experiment was repeated at Clovelly Bay and conducted at Long Reef, similar results were obtained (Fig. 3, Table 3b,c).

The mean proportional loss in numbers of *Heliocidaris* that had been transplanted to boulders without urchins (–UB + U) was significantly greater than for those translocated to boulders with urchins (+UB + U). In addition, there were no artefacts of translocating *Heliocidaris* to an unfamiliar boulder, nor disturbing them (Fig. 4; 13 June 2003: Day 1,  $F_{3,36} = 5.67$ ,  $p < 0.01$ ; Day 7,  $F_{3,36} = 11.51$ ,  $p < 0.001$ ; Day 14,  $F_{3,36} = 15.73$ ,  $p < 0.001$ ). The mean proportional change of *Heliocidaris* per boulder on each day of sampling was analysed as  $\ln(x + 2)$  of the net change in the number of *Heliocidaris* under boulders from the start of the experiment to each day of sampling. Net change =  $(N_D - N_S) / N_S$ , where  $N_D$  is the number of *Heliocidaris* under each boulder on each day of sampling and  $N_S$  is the number of *Heliocidaris* under each boulder at the start of the experiment. The actual rates of gain or loss of individuals cannot be known, because *Heliocidaris* were not tagged individually, to avoid excessive disturbance to the urchins and boulders.

When the experiment was repeated at Clovelly Bay, the number of boulders per treatment was increased to 15. After 1, 7 and 14 d, the mean proportional net loss in the numbers of *Heliocidaris* that had been transplanted to boulders without urchins (–UB + U) was significantly greater than the loss from other treatments, which did not differ significantly from each other (Fig. 4; 12 July 2003: Day 1,  $F_{3,56} = 3.44$ ,  $p < 0.05$ ; Day 7,  $F_{3,56} = 10.85$ ,  $p < 0.001$ ; Day 14,  $F_{3,56} = 7.10$ ,  $p < 0.01$ ).

Similarly, the proportion of boulders originally with urchins (+UB) that were re-occu-

pied by *Heliocidaris* was significantly greater than the proportion of boulders without urchins (–UB) that were subsequently occupied by *Heliocidaris* on each days of sampling (Day 1,  $\chi^2_1 = 7.03$ ,  $p < 0.05$ ; Day 7,  $\chi^2_1 = 7.03$ ,  $p < 0.05$ ; Day 14,  $\chi^2_1 = 12.86$ ,  $p < 0.01$ ). Results were similar at Long Reef (Fig. 3; Day 1, no data; Day 7,  $\chi^2_1 = 7.50$ ,  $p < 0.05$ ; Day 14,  $\chi^2_1 = 13.61$ ,  $p < 0.001$ ) and when the experiment was repeated at Clovelly Bay (Day 1,  $\chi^2_1 = 6.14$ ,  $p < 0.05$ ; Day 7,  $\chi^2_1 = 20.0$ ,  $p < 0.001$ ; Day 14,  $\chi^2_1 = 22.53$ ,  $p < 0.001$ ).

Furthermore, when *Heliocidaris* were transplanted to boulders that did or did not have urchins, the proportion of boulders with a net loss of *Heliocidaris* was greater for boulders that did not originally have urchins.

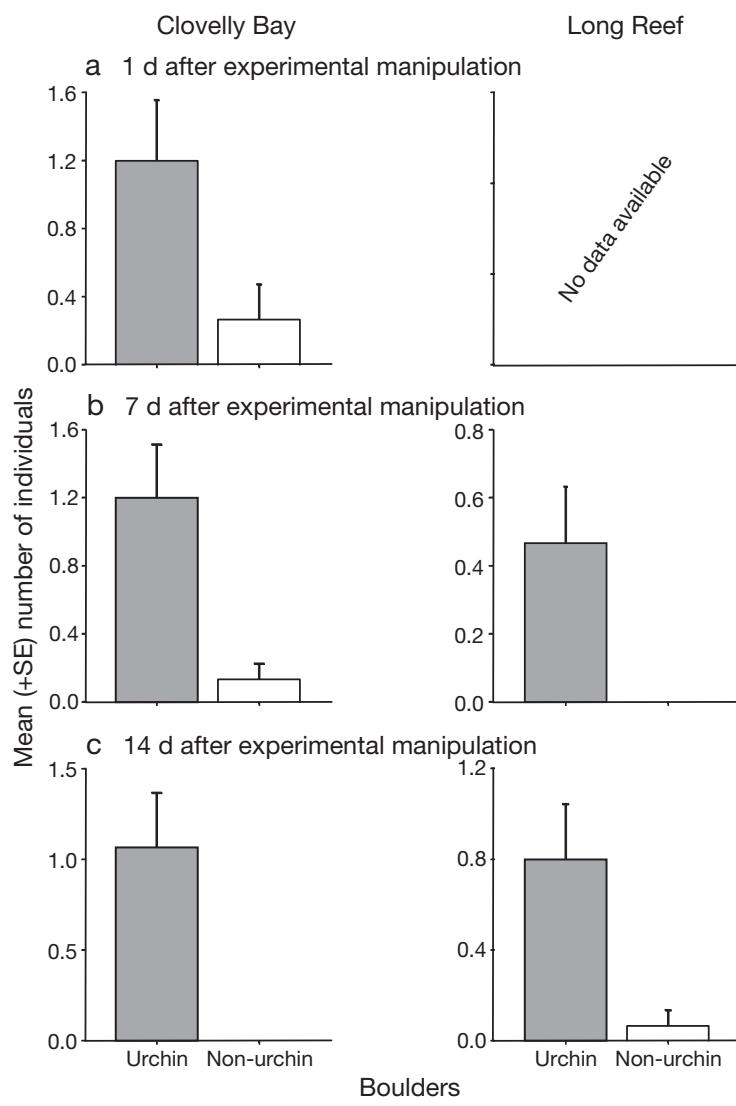


Fig. 3. *Heliocidaris erythrogramma*. Mean number (+SE) of adults that colonised 15 boulders originally with urchins (+UB) and 15 boulders originally without urchins (–UB) at Clovelly Bay on 13 June 2003 and Long Reef on 30 July 2003

Table 3. *Heliocidaris erythrogramma*. Analyses of the mean number of *Heliocidaris* that colonised boulders: (1) originally with urchins from which *Heliocidaris* were experimentally removed (+UB - U) and (2) originally without urchins (-UB) at (a) Clovelly Bay on 13 June, (b) Clovelly Bay on 12 July and (c) Long Reef on 30 July. The factor treatment is fixed with  $n = 15$ ; ns:  $p > 0.05$ ; \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Source	df	1 d after manipulation		7 d after manipulation		14 d after manipulation	
		MS	F	MS	F	MS	F
<b>(a)</b>							
Cochran's test			$C = 0.75$ ns		$C^a = 0.75$ ns		$C = 1.00$ ***
Treatment	1	6.53	5.18*	2.43	10.03*	8.53	12.62*
Residual	28	1.26		0.24		0.68	
Total	29						
SNK		+UB - U > -UB		+UB - U > -UB		+UB - U > -UB	
<b>(b)</b>							
Cochran's test			$C = 0.83$ **		$C = 1.00$ **		$C = 0.61$ ns
Treatment	1	3.33	4.22*	13.33	28.00***	7.07	82.53***
Residual	28	0.79		0.47		0.09	
Total	29						
SNK		+UB - U > -UB		+UB - U > -UB		+UB - U > -UB	
<b>(c)</b>							
Cochran's test			No data		$C = 1.00$ **		$C = 0.93$ **
Treatment	1			1.63	7.98*	4.03	8.47*
Residual	28			0.20		0.48	
Total	29						
SNK		+UB - U > -UB		+UB - U > -UB		+UB - U > -UB	

<sup>a</sup>Variances were heterogeneous and data were transformed using a fourth root transformation ( $x^{0.25}$ )

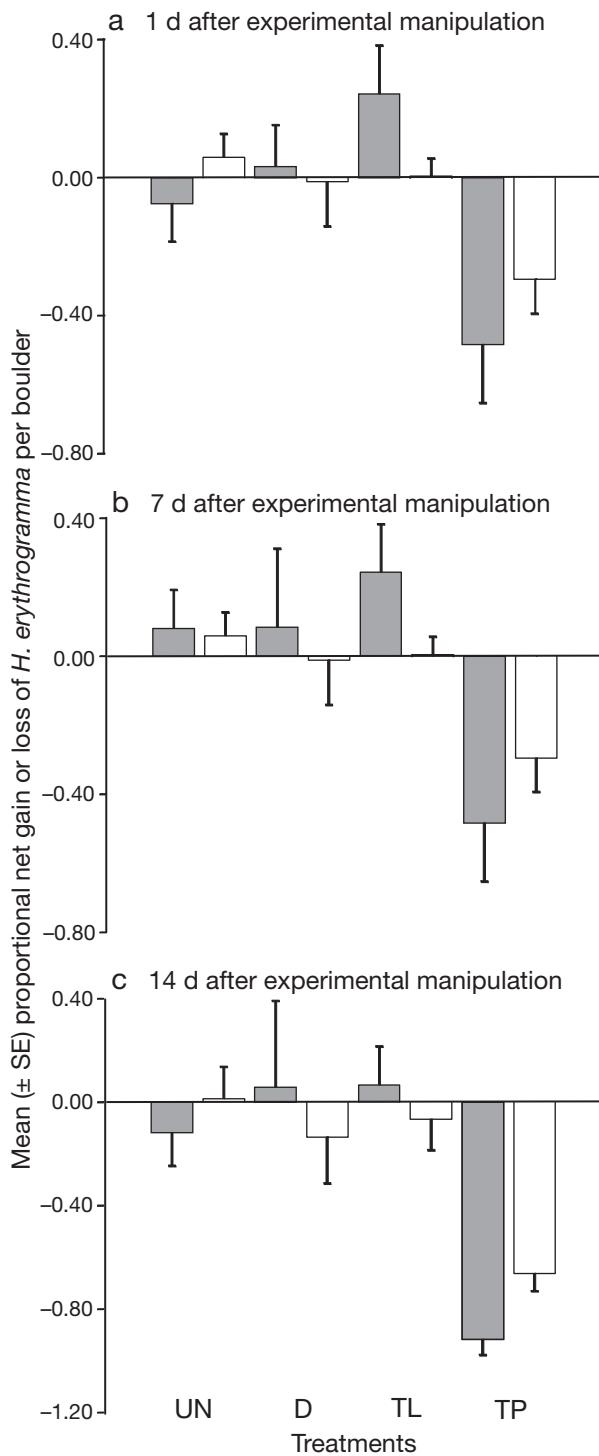
chins than for boulders that did. This result was consistent on all days of sampling (Day 1,  $\chi^2_1 = 6.11$ ,  $p < 0.05$ ; Day 7,  $\chi^2_1 = 9.86$ ,  $p < 0.01$ ; Day 14,  $\chi^2_1 = 7.12$ ,  $p < 0.01$ ) and similar results were obtained when the experiment was repeated 1 mo later at Clovelly Bay (Day 1,  $\chi^2_1 = 5.6$ ,  $p < 0.05$ ; Day 7,  $\chi^2_1 = 8.13$ ,  $p < 0.01$ ; Day 14,  $\chi^2_1 = 5.14$ ,  $p < 0.05$ ).

## DISCUSSION

Abundances of *Heliocidaris* were very different among individual boulders, such that *Heliocidaris* occupied only a subset of the available boulders within a site. This pattern was found consistently at different times and in boulder fields tens of kilometres apart. Aggregated patterns of distribution have similarly been observed for *H. erythrogramma* in South Australia (Connolly 1986) and for other species of urchins elsewhere (e.g. Russo 1979, Andrew & Stocker 1986). For example, Andrew & Underwood (1989) showed that adult *Centrostephanus rodgersii* were aggregated within crevices in barren areas during hours of daylight. Similar small-scale patterns of dispersion have also been documented for other taxa living under intertidal and shallow subtidal boulders (see Chapman & Underwood 1996, Chapman 2005). For example, Grayson & Chapman (2004) found that all chitons of

the genus *Ischnochiton* were extremely overdispersed among boulders, such that most of the boulders available were not occupied by chitons, but some boulders had very large abundances of individuals.

Patchy patterns of dispersion of organisms have frequently been explained in terms of variation in patterns of recruitment (e.g. Balch & Scheibling 2000), mortality (e.g. Connell 1961) or behavioural responses of adults to habitat and/or to conspecifics (e.g. Crowe 1996). *Heliocidaris* recruited in greater numbers to boulders with urchins than to boulders without urchins, and more boulders with adult urchins were colonised by recruits than were boulders without adult urchins. This suggests that recruitment contributes to differences in the dispersion of *Heliocidaris* among boulders. It does not, however, distinguish between responses of recruits to particular boulders (i.e. habitat) and/or presence of conspecifics. Each of these factors has been shown to affect other taxa (e.g. Tegner & Dayton 1977). If urchins had recruited to the experimental treatments designed to test hypotheses about colonisation and dispersal, we would have been able to distinguish among these factors. Unfortunately, the experiments were conducted after recruitment. Furthermore, we could not maintain the experimental treatments over periods long enough to quantify recruitment at subsequent times because adults clearly moved among boulders, thereby changing the classifi-



**Fig. 4.** *Heliocidaris erythrogramma*. Mean ( $\pm$  SE) proportional net change in the number of juveniles and adults per boulder in each treatment at Clovelly Bay on 13 June 2003 ( $n = 10$  boulders; grey bars) and Clovelly Bay on 12 July 2003 ( $n = 15$  boulders; white bars). UN: undisturbed *Heliocidaris* under boulders originally with urchins; D: disturbed *Heliocidaris* under boulders originally with urchins; TL: boulders with urchins that had *Heliocidaris* translocated from other boulders with urchins; TP: boulders originally without urchins that had *Heliocidaris* added from boulders with urchins

cation of the boulder. Therefore, we do not know how long boulders originally without urchins had no urchins and further what period of time urchins had been on boulders originally with urchins.

Nonetheless, few studies have specifically shown the relative importance of events early in the life cycle of echinoids in determining patterns of adult distributions (but see Andrew & Underwood 1989, Andrew & Choat 1985), or have been done at the small, within-habitat scale, such as the one presented here. While this study has shown that the overdispersion of *Heliocidaris* among boulders may be established early in the animals' life cycle, it is also not known whether larvae arrive in greater numbers under boulders with urchins than under boulders without urchins, or whether, similar to other echinoderms, larvae settle randomly and then succumb to differential rates of mortality (Rowley 1990) or migration (Mercier et al. 2000).

Juvenile and adult animals may also establish and/or maintain patterns of dispersion by their movements around habitats. Animals may react: (1) positively to 'favoured habitat', (2) negatively to 'unfavoured' habitat, or (3) positively to 'favoured' habitat and negatively to 'unfavoured' habitat. Past studies (e.g. Carefoot 1979) have often assumed that because a species is more abundant in a particular habitat, it prefers to be in that habitat, or that it has actively 'selected' it and rejected other available habitats. These studies often fail to define 'preference' (but see Crowe & Underwood 1998). Before conclusions can be drawn about an animal's 'preference', it is first essential to experimentally test models about aspects of movement of the animal to explain the observed pattern of distribution. These models are best tested using transplant experiments.

Here, experimental transplants demonstrated that differences in the behavioural responses of juvenile and adult *Heliocidaris* to particular boulders may strongly influence the dispersion of *Heliocidaris* among boulders. This includes rates of colonisation and dispersal of adult *Heliocidaris* to and from the 2 types of boulders, thus affecting the mean number of animals per boulder and the proportion of boulders occupied.

Adult *Heliocidaris* colonised boulders from which urchins had been experimentally removed (i.e. those that were originally 'suitable' urchin-habitat) at a greater rate than they did boulders originally without urchins. Caution must be taken when interpreting these results, as there may have been remnant chemical cues left by the removed urchins. This experiment could not incorporate a control for this potential cue because it was not possible to know whether removed urchins left some potential unknown cue, nor to remove such a cue without removing urchins. In the

absence of such controls, it is possible that *Heliocidaris* colonised boulders originally occupied by urchins because of chemical cues left by conspecifics and/or because of other features of the boulders. Given that *Heliocidaris* also colonised boulders originally without urchins, the pattern is more dynamic than may be suggested by a single time of sampling. In spite of this, this research along with that of many others (Moran 1985, Chapman & Underwood 1994) has emphasised the importance of movement, not only in maintaining an animal's distribution, by individuals moving away from potentially 'unfavourable' habitats, but also restoring their distributions when displaced from their normal habitat.

In order to test for generality of ecological processes in addition to patterns, experiments need to be replicated (e.g. Underwood 2000). In this study, the experiments were each done twice; at each time, similar results were found. The hypotheses testing predictions about the effect of colonisation were spatially replicated, but the 2 hypotheses testing predictions about the effect of dispersal could only be replicated in 1 location. There were not enough boulders occupied by *Heliocidaris* for experimental treatments and appropriate controls at Long Reef. The generality of these results should therefore be interpreted with care. Nonetheless, there is sufficient evidence to suggest that patterns of dispersion of *Heliocidaris* can be explained by behavioural responses to feature(s) of boulders and/or any cues left by previous urchins.

Boulders vary in abiotic features (e.g. colour, shape, size, composition and complexity), biotic features (e.g. assemblages of sessile and mobile organisms) and features of the surrounding environment (e.g. substratum on which the boulder rests and depth of water), which may influence the patterns of dispersion of *Heliocidaris*.

James & Underwood (1994) found that the colour of the boulders influenced the recruitment of spirorbid tubeworms. McGuinness & Underwood (1986) showed that the complexity of the surface and the material from which the boulder was made significantly affected the number and/or abundance of mobile species that colonised boulders. Similarly, Downes et al. (2000a,b) showed that the surface texture of boulders increased species richness of macro-invertebrates on boulders in freshwater systems. Size of boulders can also influence the assemblages associated with boulders by altering rates of disturbance (via overturning or burial) and/or by providing space for species to colonise the boulders (Sousa 1979, Osman 1977, McGuinness 1987). Animals and plants living under boulders are particularly vulnerable to disturbances because of the unstable and complex nature of boulders (Chapman & Underwood 1996). Physical disturbances to boulders include being moved and/or overturned by

wave-action or people (Osman 1977, Sousa 1979) and/or burial by sand and the associated sand-scouring. Although disturbance has been shown to vary at large spatial scales, i.e. among shores, the effects of disturbance may be influenced by small scale variation in features of boulders, such as size (McGuinness 1987) and depth (Osman 1977).

Boulders also vary in the assemblages of sessile and mobile species that live on them (e.g. Sousa 1979, Chapman & Underwood 1996). Chapman & Underwood (1996) showed that a diverse assemblage of encrusting and foliose algae, sessile and mobile animals and other materials were associated with intertidal boulders. These organisms and abiotic materials may potentially influence the distribution and abundance of mobile species, by providing favourable conditions, such as food, shelter, or refuge from predators (McGuinness 1988, Downes et al. 2000a,b). McGuinness (1988) showed that mobile organisms, primarily molluscs, colonised boulders with sessile organisms at a faster rate than they did boulders without sessile organisms. He considered that the assemblages of sessile species may be an important source of food for gastropods. The patterns of occupation and colonisation of boulders by *Heliocidaris* may also be explained by responses to other species that are only present on some boulders; however, Grayson & Chapman (2004) showed no effect of boulder complexity or sessile assemblages on colonisation by mobile animals.

Andrew & Stocker (1986) found that the rate of migration of the sea urchin *Evechinus chloroticus* was a result of manipulating the availability of food, as has been documented for other species of sea urchins (e.g. Russo 1979). While these studies have documented variation in behaviour at larger spatial scales, i.e. between habitats, it is reasonable to suggest that similar processes may operate to determine the observed response of *Heliocidaris* at small spatial scales, i.e. among individual boulders, if potential food sources are only present on some boulders.

In intertidal and subtidal boulder fields in New South Wales, *Heliocidaris* appears to demonstrate specific requirements for habitat at small spatial scales, using only a subset of boulders in any place. Understanding the feature(s) of habitat to which *Heliocidaris* responds will only be possible once more detailed experimental tests are done. This study suggests directions of such tests. Specifically, novel experimental protocols are needed to successfully separate the importance of features of boulders and cues associated with urchins, independent of their presence. Until more is known about the importance of these factors, however, conservation and management of *Heliocidaris* and its habitat should take account of variation at the small scales identified within this study.

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