The use of sandstone blocks to test hypotheses about colonization of intertidal boulders

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This study tested the hypothesis that regularly-shaped sandstone blocks in intertidal boulder-fields are colonized by mobile macrofauna at a similar rate to colonization of natural boulders. In addition, the sessile component on these plates (three levels of sessile assemblages) and their position in the boulder-field (three different positions relative to other boulders) were varied to test hypotheses about effects of these features on colonization. The epibiota varied among the three sets of plates and the natural boulders at the start of the experiment. The boulders were very rapidly colonized by a suite of mobile animals, particularly chitons, gastropods and echinoderms. Colonization was sparse and patchy to start with, causing great variability among replicates. Nevertheless, it did not differ among any of the treatments, indicating that even at this early stage, colonization did not differ between natural boulders and blocks, nor according to the sessile assemblage, or the proximity of other boulders. By six months, there was little variability among replicates and the assemblages had converged. This indicates that sandstone plates/blocks can form a standardized unit of habitat which can be used to test models about spatial variation in this relatively specialized fauna.

INTRODUCTION

Intertidal boulder-fields in New South Wales, Australia are not particularly common habitats. Nevertheless, they support a diverse range of marine organisms. Some species live on the boulders themselves (e.g. McGuinness & Underwood, 1986; Chapman, 2002). Others live on or amongst other organisms (e.g. algal mats growing on the boulders; Dean & Connell, 1987). Although some species, particularly those found on the upper surfaces are common to other intertidal habitats (e.g. rock-platforms; Sousa, 1979a,b; McGuinness & Underwood, 1986), other species are relative specialists, only, or predominantly, found in association with boulders. These are usually associated with the undersurfaces of the boulders (e.g. McGuinness & Underwood, 1986; Chapman, 2002a and references *loc cit*).

The most common larger mobile macrofauna living under intertidal and shallow subtidal boulders in New South Wales are gastropods, chitons and echinoderms (Chapman & Underwood, 1996; Smith & Otway, 1997; Chapman, 2002a). They are generally extremely over-dispersed, in that, in any site, most species are very abundant on very few boulders and absent from most (Chapman, 2002a). Nevertheless, few boulders are entirely unoccupied by any species, indicating that most boulders can provide a habitat for these animals, although most species are not found on the majority of boulders.

Boulders vary in physical features (e.g. size, shape, complexity, composition), biotic features (e.g. the assemblages living on them) and their local environment (e.g. proximity of other boulders, depth of water, etc.). Although many of these factors influence colonization in other habitats, relatively few have been examined for boulders. Nevertheless,

size of the boulder can influence the associated assemblage, by providing space for colonization and/or by influencing its disturbance regime (via burial or overturning; e.g. Osman, 1977; Sousa, 1979a,b; McGuinness, 1987a,b). Settlement on boulders was also affected by colour of the substratum (e.g. James & Underwood, 1994). Nevertheless, in lowshore and shallow subtidal boulder-fields around Sydney, NSW, little variation in abundance of mobile fauna on boulders can be explained by the size of the boulder (Chapman & Underwood, 1996; Chapman, 2002a) and there are no consistent patterns of correlation among abundances of different species of mobile animals, nor between them and the sessile assemblage (McGuinness, 1987a).

The logical method to identify which of the many features of boulders and their surroundings influence assemblage of animals living under them is to use experimental manipulations, by which some factors are kept constant while others vary. Osman (1977) compared colonization of experimental plates to that on natural boulders to compare the effect of size of patches of habitat on colonization. McGuinness & Underwood (1986) showed that many species living on intertidal boulders colonized concrete blocks and colonization was affected by the thickness of the blocks and the diversity of microhabitats added to their surfaces. The use of concrete blocks allowed sizes and microhabitats to be controlled. These experiments were done at mid- to high-shore levels and the mobile animals that colonized these habitats were common species on the surrounding rock platform. Neither studies specifically discussed colonization by animals that are predominantly (or only) found under boulders.

Previous work in lowshore and shallow subtidal boulder-fields showed that recently quarried sandstone

boulders were rapidly colonized by a wide range of invertebrates (Chapman, 2002b), including species predominantly found under boulders. These quarried boulders had complex and variable surfaces and varied in size. If regular blocks are also colonized by specialist species similarly to natural habitat, it would be possible to provide 'boulders' of different sizes, complexity, composition, etc. to test experimentally complex hypotheses about colonization of boulders by specialists. This experiment tests the hypothesis that regular sandstone blocks, with minimal surface features, are colonized by mobile macrofauna in a similar manner (with respect to abundances and diversity) as are natural boulders. These blocks were of consistent size, shape and surface complexity and had the same area of undersurface as the average for natural boulders.

In addition to varying in physical features, natural boulders differ in the amounts and types of algae and sessile animals on their surfaces (e.g. Sousa, 1979; Chapman & Underwood, 1996). These organisms may influence abundances of mobile species by providing food or habitat (e.g. Dean & Connell, 1987; McGuinness, 1988). To test the hypothesis that the sessile assemblage living on the undersurface of a boulder will alter rates of colonization by mobile fauna, sandstone blocks were 'seasoned' prior to the experiment by caging them on a shallow subtidal reef for six or nine months prior to the start of the experiment. They developed a cover of algae, bryozoans, tubeworms and other sessile fauna, which resembled that found on the natural boulders in these lowshore study sites. Colonization of these by mobile fauna was compared to that of new sandstone blocks (with no initial associated assemblage) and natural boulders.

The position of boulders in a boulder-field may also influence colonization, as shown for *Ischnochiton* spp. (Grayson, 2001) and microgastropods (Chapman, 2002b). This may be due to the substratum on which the boulder rests (Chapman, 2002b), or proximity to other occupied boulders. The latter may be especially important for mobile macrofauna such as chitons or gastropods, which may not, as adults, move through the water column, or over the sandy matrix surrounding boulders. To test the hypothesis that proximity to natural boulders will influence colonization, fresh and 'seasoned' blocks and defaunated boulders were placed adjacent to natural undisturbed boulders, or approximately one metre away (the average distance among boulders in the study site). To test the hypothesis that particular positions in boulder-fields increase colonization (e.g. Grayson, 2001), fresh and 'seasoned' blocks and defaunated boulders placed 1 m from natural boulders, were placed either in a position previously occupied by a boulder (which was removed) or in a position not occupied by a boulder at the start of the experiment. Because of loss of some blocks, there were not enough replicates for all treatments and the blocks seasoned for nine months were not placed in a previously occupied position.

Therefore, there were four sets of colonization surfaces, blocks 'seasoned' for nine (Set 1) or six (Set 2) months, fresh sandstone blocks (Set 3) and natural boulders (Set 4). These were placed adjacent to a natural boulder (Position 1), or in a position further away which was occupied (Position 2, excluding blocks 'seasoned' for nine months) or was not occupied (Position 3) by a boulder at the start of the experiment.

MATERIALS AND METHODS

Study site and field methods

This experiment was carried out in the intertidal/shallow subtidal boulder-field (Cape Banks, northern shore of Botany Bay, NSW, 34º00′S 150º15′E) described in McGuinness & Underwood (1986) and Chapman & Underwood (1996). Prior to the experiment, sandstone blocks were caged on nearby rocky substrata in about 2 m of water. Subtidal sites were used to minimize damage to the blocks and cages during high seas. These blocks were smooth-cut and 30×30×4 cm thick, which provided an undersurface within the range of that provided by natural boulders. Small (2 cm high) sandstone legs were glued to two adjacent corners to keep the undersurface of the block slightly off the substratum and prevent burial of this surface. In the cages, the blocks were stacked vertically with approximately 2 cm between adjacent blocks. The mesh was coarse enough to permit small urchins, starfish, snails, etc., to enter the cages. The surfaces of the sandstone blocks were rapidly colonized by a suite of algae and sessile and mobile animals. Sixteen blocks were 'conditioned' in this manner for nine or six months prior to the start of the experiment, although damage to the blocks reduced N to 8 and 12, respectively (Sets 1 and 2, respectively).

At the start of the experiment, all mobile animals were removed from the blocks and 18 natural boulders. The percentage cover of sessile animals and algae on the undersurface of each structure was estimated from 25 random points. These were not identified to species, but grouped into broad taxonomic groups as per Chapman & Underwood (1996), i.e. foliose algae, encrusting algae, sponges, tubeworms, etc. Blocks or boulders within each set were randomly allocated to positions, with N=4 for blocks (excluding Set 1 in Position 2) and N=6 for boulders. The length and width of the undersurface of each natural boulder was measured to the nearest cm. Each structure was then individually marked with two small metal tags screwed into the upper surface before being placed in the field.

At each sampling time, each block and experimental boulder was carefully overturned, the mobile animals on the undersurfaces identified and counted and the block/boulder carefully replaced in its original orientation and position. When blocks or boulders had been naturally overturned, the new undersurface was sampled and the boulders replaced in the orientation in which they had been found. Each block/boulder was sampled one day, one week and then monthly for nine months after the start of the experiment, sampling the same structures each time.

Analyses of data

At the start of the experiment, the sessile assemblage underneath each block/boulder was compared among Sets 1 (nine months 'seasoning'), 2 (six months 'seasoning') and 4 (defaunated boulders). Set 3 was 100% bare because

it was a new block. This tested the hypothesis that there would be differences in sessile assemblages for blocks conditioned for different periods of time, but blocks conditioned for nine months would be similar to natural boulders. Analysis of similarities (ANOSIM) was used on Bray-Curtis dissimilarities (Bray & Curtis, 1957) calculated from untransformed measures of percentage cover and the patterns were illustrated using nMDS plots (Clarke, 1993). Analysis of similarities was similarly used to compare the mobile assemblage colonizing the treatments after the different periods of time. The nMDS plots were used to illustrate these differences and follow changes in the colonizing assemblages among the different treatments. Data could not be analysed through time because the same replicates were examined each time. Therefore, temporal trends were illustrated graphically.

To test the hypothesis that the time course of colonization would differ among treatments, the numbers of each species in the assemblages for each set of replicates were averaged to give a centroid for each treatment. A Bray-Curtis dissimilarity matrix was calculated for differences among all times of sampling for each combination of sets and treatments separately, using untransformed data. These summarized the multivariate differences in assemblages among all of the times of sampling. These were then compared among Sets and Positions using 2-stage ANOSIM and nMDS (Somerfield & Clarke, 1995), which specifically tests the null hypothesis that relative differences in assemblages among the different times of sampling do not differ among treatments.

I predicted that proximity to occupied boulders or position in the boulder-field might have a bigger effect on colonization soon after new habitat was provided compared to later. Therefore, treatments were compared for 6-month 'seasoned' and new blocks and natural boulders in each position in the boulder-field at one, three, six and nine months after colonization. Blocks 'seasoned' for nine months were omitted from the analyses because they were not used for Position 2. Numbers of taxa and abundances of gastropods and chitons were separately analysed using analyses of variance on untransformed data. Sets and Positions were fixed factors, $N=4$ (with natural boulders chosen randomly from those available).

RESULTS

Comparisons among habitats at the start of the experiment

The natural boulders used in the experiment had a mean undersurface area of 927 (±67 SE) cm^2, compared to 900 cm^2 for the blocks, so the average area available for colonization was similar across sets. At the start of the experiment, the undersurfaces of different habitats had significantly different sessile biota (ANOSIM, Global $R=0.41$, $P=0.01$; all pair-wise comparisons $P<0.05$), although there was large variation within sets. Sets 1 and 2 (the 'seasoned' blocks) were more similar to each other than either was to Set 4 (the natural boulders), although the nine month 'seasoned' blocks tended to be intermediate between the two other habitats (Figure 1). Differences from one set to another were primarily due to cover of bare space, encrusting algae, bryozoans and encrusting worms. Both sets of 'seasoned' blocks had smaller diversity
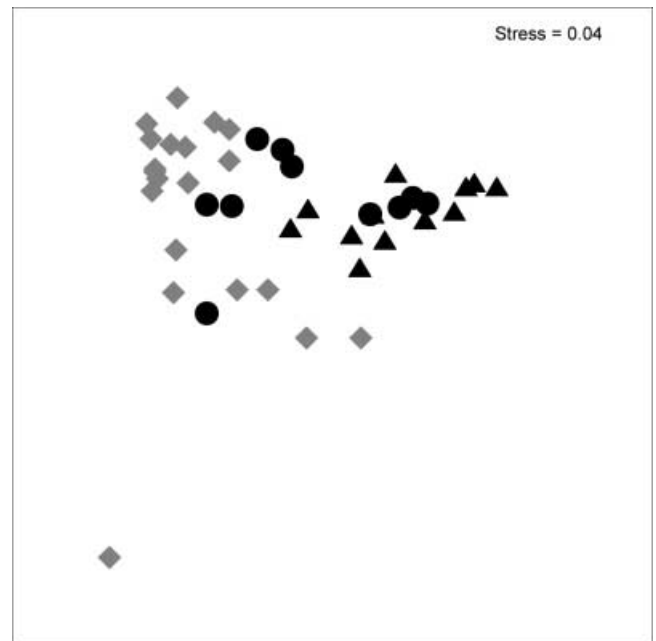
Figure 1. The nMDS plot of dissimilarity of the sessile assemblages under (●) blocks 'seasoned' for nine months, (▲) blocks 'seasoned' for six months and (◆) natural boulders at the start of the experiment.

of biota and more bare space than did the natural boulders. Despite the significant differences among Sets, they were all primarily covered with encrusting tubeworms or bare space (Table 1).

Patterns of change in abundances and numbers of taxa

One hundred and twelve taxa colonized the blocks and boulders during the experiment, of which all except platyhelminths and nematodes were identified to species (or morphospecies, *sensu* Oliver & Beattie, 1996). More than 85% of these taxa were mollusca and echinoderms. Six taxa colonized the habitats within one day of deployment; the gastropods *Nerita atramentosa*, *Austrocochlea porcata*, *Turbo undulatus*, *Clanculus brunneus*, *Gena impertusa* and Columbellidae (which were not identified further). These all arrived as adults, not as settling larvae. The first two species are common on and under boulders and on the

Table 1. *Mean (SE) cover of bare space and sessile biota on the undersurfaces of all sets of boulders at the start of the experiment; $N=4$.*

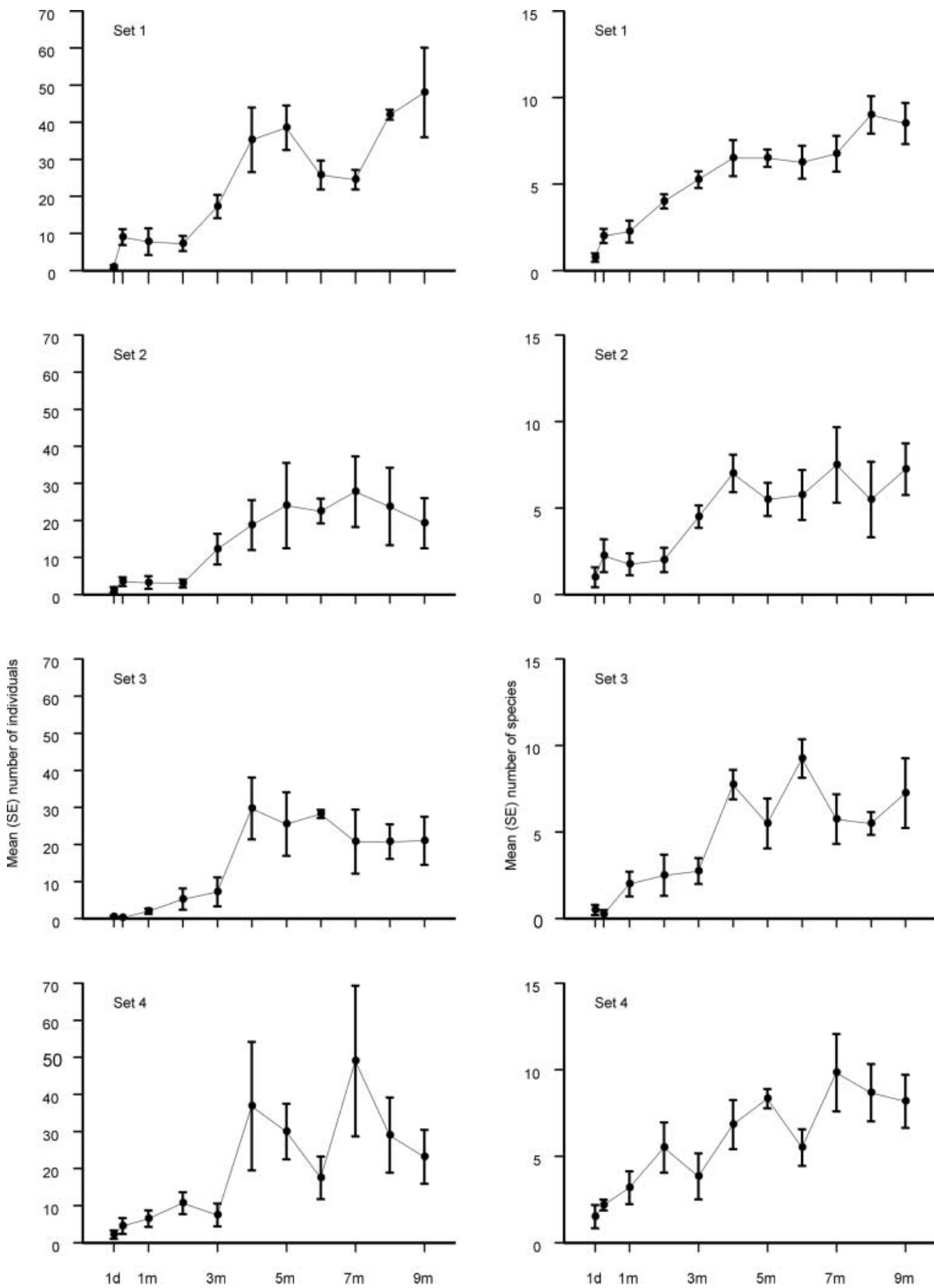|	Set 1	Set 2	Set 3	Set 4
Bare space	36.8 (7.4)	58.3 (5.5)	100.0 (0.0)	8.8 (2.7)
Foliose algae	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.2 (4.2)
Encrusting algae	8.0 (3.2)	6.0 (1.9)	0.0 (0.0)	17.4 (3.1)
Ascidians	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)
Bivalves	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.4 (0.7)
Bryozoans	8.0 (2.5)	8.7 (2.1)	0.0 (0.0)	2.6 (1.4)
Sponges	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.0 (0.8)
Tubeworms	47.2 (5.8)	26.7 (3.4)	0.0 (0.0)	63.6 (5.9)

Figure 2. Mean (SE) number of individuals and taxa per block/boulder at each time of sampling for each Set of blocks/boulders in Position 1, i.e. placed adjacent to an undisturbed boulder; N=4 for Sets 1–3, N=6 for Set 4.

Table 2. *Analyses of total number of taxa, abundances of chitons and abundances of gastropods after one, three, six and nine months;*
$N=4$; *=$P<0.05$.

Source	df	No. taxa		No. chitons		No. gastropods	
		MS	*F*	MS	*F*	MS	*F*
1 month							
Set=S	2	0.083	0.03	0.028	0.10	56.583	5.31*
Treatment=T	2	1.083	0.34	0.111	0.41	1.583	0.15
S×T	4	0.292	0.09	0.528	1.97	2.667	0.25
Residual	27	3.23		0.269		10.657	
3 months							
Set=S	2	10.028	3.41*	1.083	1.30	413.03	2.55
Treatment=T	2	6.028	2.05	0.750	0.90	311.11	1.92
S×T	4	3.069	1.04	1.458	1.75	482.78	2.98*
Residual	27	2.944		0.833		161.86	
6 months							
Set=S	2	9.333	2.02	1.028	0.75	451.19	2.16
Treatment=T	2	0.333	0.07	0.194	0.14	272.11	1.30
S×T	4	2.792	0.61	1.944	1.42	87.49	0.42
Residual	27	4.611		1.370		209.10	
9 months							
Set=S	2	0.444	0.03	0.194	0.10	17.86	0.06
Treatment=T	2	2.528	0.19	2.194	1.11	252.53	0.92
S×T	4	1.819	0.14	4.069	2.06	307.49	1.12
Residual	27	13.102		1.972		275.56	

adjacent rock platform; *Turbo* are more sparse intertidally, but are common under and around the natural boulders in the study site. *Gena* and *Clanulus*, in contrast, are seldom found in intertidal habitats other than underneath boulders on this shore. Colonization was sparse and patchy, with no apparent pattern among Positions or Sets.

After one week, a variety of taxa had colonized the blocks/boulders, including limpets (*Cellana tramoserica* and *Montfortula rugosa*), whelks (e.g. *Agnewia tritoniformis* and *Morula marginalba*) and a variety of grazing gastropods, opisthobranchs and chitons. As time increased, the general pattern was for increasing abundances of the early colonizers, with more and more species arriving in small numbers. Many individuals arrived as adults, apparently having moved across the intervening space to the new patch of habitat, but some appeared to be juvenile recruits, e.g. 77 small limpets (*Patelloida mufria*) arriving on a single block between one and three months.

Rates of colonization over the experimental period are shown for all individuals and all taxa for all sets of structures in Position 1 (i.e. placed adjacent to a natural boulder) in Figure 2. Colonization was relatively slow until about two to three months, but thereafter increased more rapidly. There were no clear differences among the different sets of structures, but the numbers and types of animals present were very variable among times. This indicates that there was variable turnover of individuals under the different blocks/boulders from time to time because the same blocks/boulders were sampled each time.

There were no significant differences in the numbers of taxa at any time of sampling, except after three months, when there were significant differences among Sets (Table 2). Student–Newman–Keuls tests were not,

however, able to identify significant differences among these (mean (SE)=4.67 (0.40), 2.92 (0.47) and 4.25 (0.64) for Sets 1–3, respectively). The mean number of taxa for each treatment are illustrated for one and nine months in Figure 3.

There were no significant differences in the abundances of chitons at any time of sampling (Table 2). Abundances were always small and patchy (Figure 3; range 0–5 individuals per replicate).

Numbers of gastropods differed among Sets, but not Positions at one month (Table 2), with significantly more gastropods on boulders than on 6-month 'seasoned' or 'unseasoned' blocks (Figure 3). Blocks 'seasoned' for nine months were not included in the analysis, but the mean abundances for the two Positions for which there were data indicated similar abundances to natural boulders (Figure 3). After three months, there was a significant Set×Position interaction (Table 2), with significantly more gastropods per boulder on the 'unseasoned' blocks which had been placed in previously occupied positions (Position 2; 35.25 (17.11)) compared to all other combinations of Sets and Positions (between 2.75 (0.80) and 18.25 (5.25)). After six and nine months, there were no significant differences among treatments (Table 2; illustrated for nine months in Figure 3).

Changes in the mobile assemblages through time

The assemblages of mobile animals were compared among Sets and Positions, one, three, six and nine months after the start of the experiment (data prior to one month were very sparse) using ANOSIM. There was no general pattern of variation between Sets (the different symbols in Figure 4), nor between the different Positions
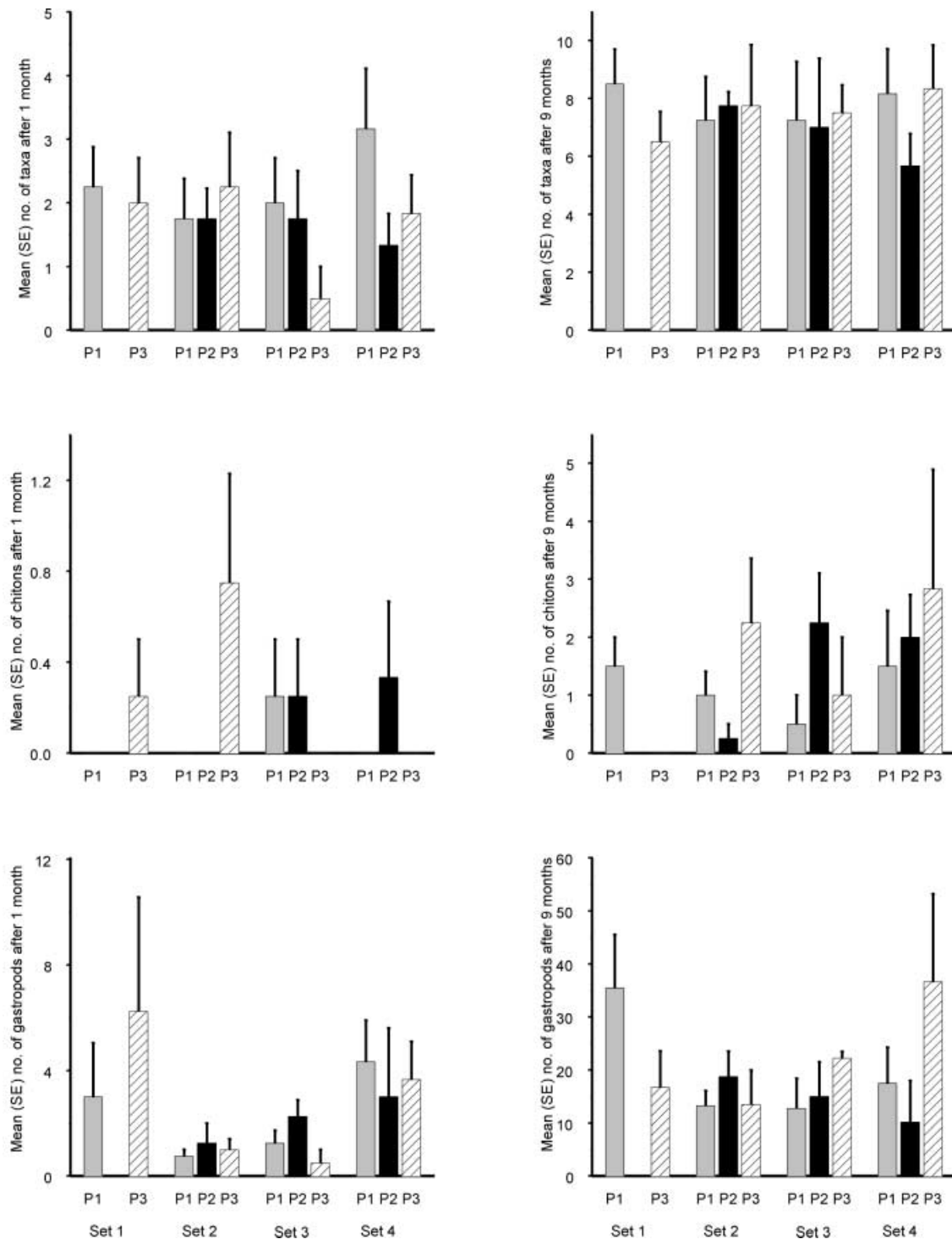
Figure 3. Mean (SE) number of taxa, chitons and gastropods per block/boulder for each Set and Position after one and nine months of colonization; N=4 for Sets 1–3, N=6 for Set 4.

(the different sizes of symbols in Figure 4). Therefore, between one and nine months after the experiment started, although there were some differences in abundances of broad groups of taxa, the assemblage of mobile animals under the boulders was not generally influenced by the type of habitat provided (i.e. natural boulder or blocks), its proximity to other boulders, nor whether it had been placed in the site of another boulder or not.

The centroids for each treatment (i.e. combination of Set and Position) showed a general pattern of convergence through time (see nMDS plots in Figure 5). Therefore, although the assemblages did not generally differ among treatments at one, three, six and nine months, they became more similar as the period of colonization lengthened. This is illustrated for periods of one day to six months for the four Sets of structures placed adjacent to
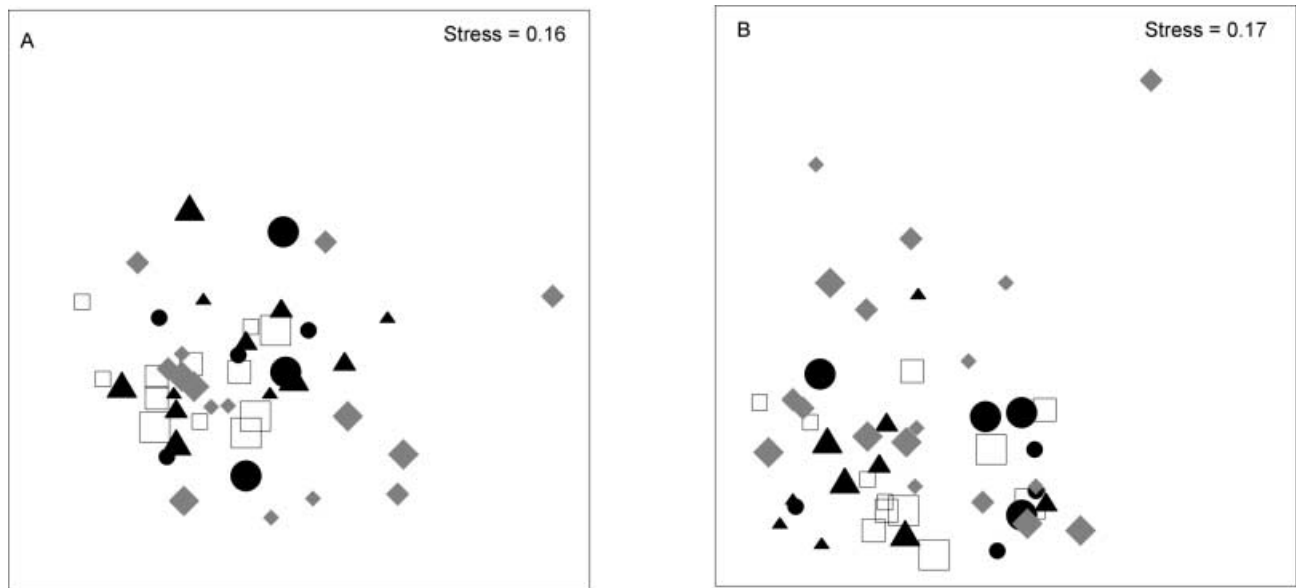
Figure 4. The nMDS plot of dissimilarity of the colonizing mobile assemblages after (A) three months; and (B) six months found underneath (●) blocks 'seasoned' for nine months, (▲) blocks 'seasoned' for six months, (□)m 'unseasoned' blocks and (◆) natural boulders (treatments with zero animals omitted). The increasing size of the symbols represent Positions 1–3, respectively.
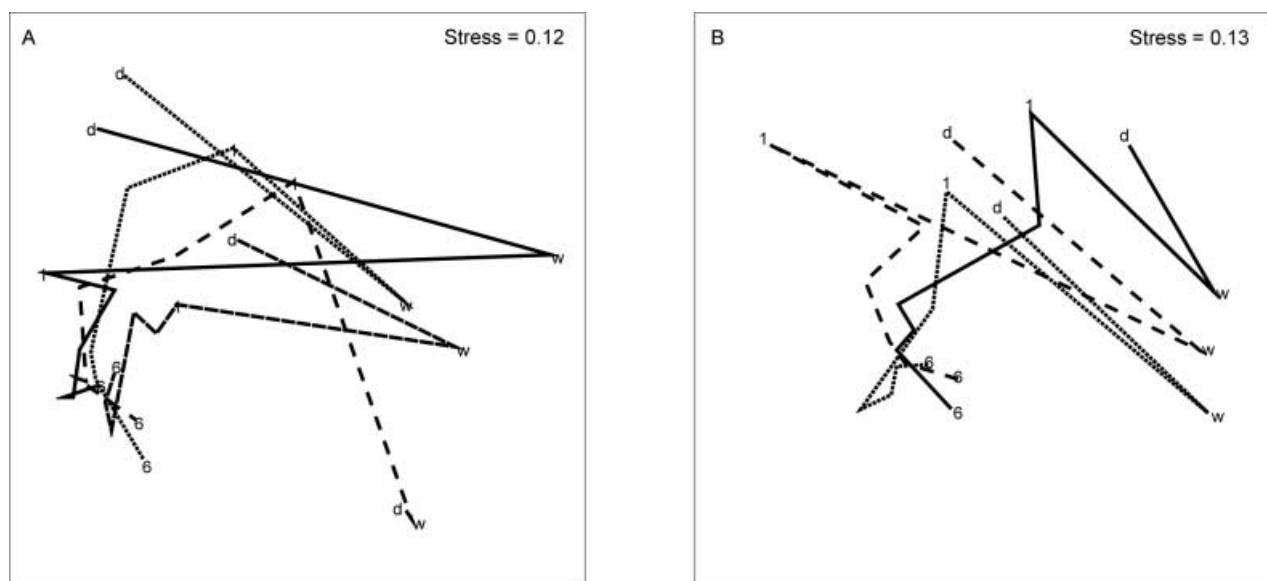

Figure 5. The nMDS plots of changes through time between one day and six months for (A) each Set placed adjacent to boulders; and (B) the different Positions for blocks 'seasoned'; data are centroids for each treatment. d, 1 day; w, 1 week; 1, 1 month; 6, 6 months.

boulders in Figure 5A and for the different positions for blocks 'seasoned' for six months in Figure 5B. The convergence was maintained between six and nine months. These data were not, however, included in the Figure because the many small overlapping changes caused the main trend to be difficult to discern.

Despite the convergence of the assemblages, the 2-stage ANOSIM which compared relative magnitude of the changes in assemblages through time showed a significant difference among Treatments and Sets (1-factor ANOSIM,

$R=0.191$, $P<0.05$). Nevertheless, pairwise differences among all combinations of Sets and Treatments gave no consistent patterns, although 12 of the 15 significant pairwise differences ($P<0.05$) were between natural boulders and blocks. Colonization of natural defaunated boulders appeared therefore to follow a different time course to that of blocks, generally because boulders were more rapidly colonized in the early stages (refer to Figure 2). These differences were not, however, very large and, in general, all sets were colonized by similar assemblages over time.

DISCUSSION

There is considerable advantage in using artificial units of habitat to test experimentally many ecological hypotheses because the units can be standardized, except for specific characteristics and they can be deployed in densities, positions, etc. to allow balanced experimental design. Artificial substrata have been used to mimic seaweeds (Myers & Southgate, 1980; Edgar, 1991), sea grasses (Jenkins et al., 1998; Bologna & Heck, 1999) or to create new habitats (Bombace et al., 1994; Bartol & Mann, 1997). Flat plates or blocks of material have similarly been used to examine fouling (e.g. McGuinness, 1989) or development of assemblages in different habitats (e.g. Keough, 1983; Glasby & Connell, 2001). Often, the plates/blocks are made of unnatural material, e.g. perspex, whereas in other studies, they are considered to be representative patches of natural habitats and are therefore made of stone or coral. In such studies, although the plates/blocks are discrete patches (i.e. Type I patches; Sousa, 1985), they are considered to be representative of more extensive habitat (McGuinness, 1989; Glasby & Connell, 2001).

In boulder-fields, the boulders are discrete patches of habitat, often separated by a different matrix of habitat (e.g. sand or mud, i.e. Type II patches; Sousa, 1985). Species living on or under boulders are extremely overdispersed, with very large numbers of any particular species on very few boulders (Chapman & Underwood, 1996; Chapman, 2002a). Explanations of variation in assemblages among boulders include differences in colonization and mortality in response to features of the boulders themselves (e.g. other components of the assemblage (Dean & Connell, 1989), size (Osman, 1977), colour (James & Underwood, 1994) or complexity of the surface (McGuinness & Underwood, 1986)), or where boulders lie with respect to substratum (Chapman, 2002b) or disturbance by waves (Sousa, 1979a,b; McGuinness, 1987a,b). Many features of boulders are naturally confounded (e.g. size and associated epibiota (Sousa, 1979a,b)) and spacing between boulders can vary with size of the boulder and position in the boulder-field. Using artificial blocks of stone to represent boulders has allowed complex experiments to test hypotheses about colonization of boulders, with replication at appropriate spatial and temporal scales (e.g. McGuinness & Underwood, 1986). The value of such results depends on similarity of responses of organisms to artificial habitats and natural boulders (McGuinness, 1989).

In this study, colonization by mobile invertebrates onto sandstone plates (of the same material as natural boulders) was compared to that of natural defaunated boulders. The plates were of similar size to natural boulders and were deployed in the boulder-field in the spaces amongst the boulders. In contrast to the natural boulders, however, the plates had no visible surface features and had three levels of associated epibiota at the start of the experiment; none or a covering of encrusting and foliose algae and sessile animals, which had developed over six or nine months. These epibiota varied significantly over all treatments, with more bare space on all of the plates. Therefore, either nine months was not adequate time, or the surface features of plates were not suitable for a natural epibiota to develop. This contrasts with McGuinness (1989), who

showed fewer species colonizing plates after a few months compared to natural clearings on coral reefs, but, by seven months, differences were small and inconsistent.

Many mobile molluscs vary in abundances at small spatial scales, much of which is explained by responses to small-scale variation in physical features of habitat or patterns of other organisms (e.g. Underwood, 1976; Chapman, 1994; Jernakoff, 1985; Worthington & Fairweather, 1989; Underwood & Chapman, 1996). A diverse mobile assemblage colonized the plates and boulders, including, sipunculids, nemerteans, sea anemones, chitons, gastropods and various echinoderms. Most were gastropods, which also form the majority of the macrofauna ($>5\,mm$) living on the undersurfaces of natural boulders (Chapman & Underwood, 1996). Colonization occurred within a week, although it was sparse and patchy to start with. Densities and diversity gradually increased, but the variable numbers and diversity from time to time showed that many species arrived and left the plates/boulders during the experiment. In contrast to what was predicted, there were no consistent differences in diversity or densities of colonists according to the type of habitat presented. Therefore, there was no evidence that the diversity of sessile biota, or the complexity of the surface of the structure, influenced either the types or numbers of mobile animals moving onto the undersurfaces of them. This contrasts with McGuinness (1988) who showed that more species of mobile animals colonized boulders with sessile epibiota than those without epibiota. Although his experiments were carried out in the same boulder-field, they were higher on the shore, where the boulders were frequently disturbed by waves. A number of studies have shown increased diversity on boulders of sessile (Sousa, 1979a,b) and mobile (McGuinness, 1987a,b) animals at intermediate levels of disturbance.

In addition, in contrast to what was predicted, colonization was not affected by proximity to other boulders. This was surprizing because the boulders were separated by sand and many of these species, particularly chitons, sea anemones and many gastropods, are not generally seen on sand. Grayson (2001) showed, however, that *Ischnochiton* spp., which are generally confined to the undersurfaces of boulders during the day, move out into surrounding habitat at night, presumably to feed. They can also be found attached to small pieces of stone under the sediment. More extensive movement among boulders than one might expect from patterns of distribution during the day could explain the variation in numbers/diversity of taxa on individual boulders/plates from one time of sampling to the next, in addition to the absence of any effect of proximity to other boulders.

In conclusion, many species living under boulders are uncommon in other habitats. In boulder-fields, they are very overdispersed, suggesting strong responses to localized features of habitat or environment. Because boulder-fields are not very common along the coast of NSW, many of these species are also relatively uncommon. In addition, boulder-fields are subjected to many natural and human disturbances, which may thus adversely affect populations of potentially vulnerable species. In order to manage these species and their habitats, or to restore habitat after degradation, it is important to understand the environmental cues that cause such strong patterns of overdispersion.

This is best achieved using field experiments. This study showed that this fauna readily colonized artificial blocks of stone, although they had few surface features that may act as cues, compared to natural boulders. At the start, assemblages were patchy and sparse, causing considerable variation among replicates, but similarly over all treatments. Over a few months, the assemblages on all the different treatments converged. Sandstone plates/blocks do, therefore, form a standardized unit of habitat, which can be used to examine processes influencing the assemblage of these specialized mobile animals.

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