Constructing replacement habitat for specialist and generalist molluscs — the effect of patch size

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ABSTRACT: Urban shorelines are threatened by 'armouring' from anthropological constructions that are replacing the natural intertidal habitat at an increasing rate. In places, intertidal boulder fields are listed as threatened habitats in urbanized areas. On sheltered shores, these habitats support diverse assemblages, including specialist species, many of which are rare that predominantly or only live under boulders. Activities associated with urbanization threaten these habitats and this specialist biota. Thus, there is a need to learn how to restore these habitats for these assemblages. Most studies of intertidal habitat replacement have focused on habitats dominated by large plants, e.g. mangroves, or by animals that create habitat, e.g. oyster reefs, although previous work has shown that invertebrates will colonize newly created patches of quarried boulders. Here, colonization of newly created patches, either of 50 (50B patches) or 100 (100B patches) quarried boulders replicated in 2 intertidal sites in New South Wales, Australia, is described. Rare specialist and common widespread animals readily colonized these patches, with most of the species randomly distributed between the patch sizes. Of those that did show differences between patch sizes, some species were more abundant on the 100B patches, whereas other related species showed the opposite pattern. After a few weeks, most of the species were as abundant in these patches as on natural boulders. There was no consistent tendency for abundances or diversity to be smaller on the artificial patches than on natural boulders. It is clearly cheap and easy to build an intertidal boulder habitat which is rapidly used by many different common and rare animals. This may assist with the conservation of these fauna living in urbanized environments, where much of their natural habitat has been lost.

KEY WORDS: Boulders · Habitat creation · Habitat loss · Disturbance · Intertidal assemblages · Urbanization

INTRODUCTION

With expanding urbanization worldwide, especially in coastal areas (Erdle et al. 2006, Airoldi & Beck 2007), intertidal shorelines are increasingly being lost or modified by urban infrastructure (Thompson et al. 2002, Bilkovic et al. 2006, Erdle et al. 2006, Bulleri & Chapman 2010). Kilometres of novel habitats have been added to existing shorelines, e.g. seawalls (Chapman 2003a), floating pontoons (Holloway & Connell 2002), marinas, piers and shaded walkways (Able et al. 1998, Clynick 2006)

and docks (Russell et al. 1983). Many artificial habitats do not support assemblages of species similar to those which occur in natural habitats, e.g. intertidal seawalls (Chapman 2003a), pilings (Glasby 1999) and marinas (Burdick & Short 1999, Clynick 2006). Yet, despite documented negative impacts of coastal 'armouring' on intertidal and nearshore assemblages, it continues. Increasing urbanization, with potential effects of climatic change on sea levels and storms, will inevitably lead to more, rather than fewer, armoured and unnatural shorelines (Bulleri & Chapman 2010).

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Simultaneously, there is increasing recognition that conservation cannot be guaranteed if efforts are confined to the few natural reserves that have been established, but must be part of the environment in which 'people live and work' (Miller & Hobbs 2002, Rosenzweig 2003). People demand access to areas rich in local biodiversity (Dearborn & Kark 2010), so there is a need to conserve biodiversity in and near cities (Miller & Hobbs 2002, Luck 2007). Because urban habitats are, however, profoundly altered, nature conservation in cities often requires some degree of habitat rehabilitation, although opportunities are often limited. Hence, more research is needed to determine how one can adapt or rehabilitate the novel habitats that are emerging with urbanization to sustain biodiversity in such areas (Hobbs et al. 2006, Chapman & Underwood 2011), an approach that has been termed reconciliation ecology (Rosenzweig 2003) or ecological engineering (Mitsch & Jørgensen 2004).

Habitat rehabilitation in the marine environment has generally focused on habitats dominated by large animals or plants — often species which create habitat for other species or strongly modify the environment (Seaman 2007). These include coral reefs (Epstein et al. 2003), oyster reefs (Rodney & Paynter 2006), mangrove forests (Field 1999), saltmarshes (Zedler 1996), kelp forests (Hernández-Carmona et al. 2000) and seagrass beds (Pranovi et al. 2000). Rehabilitation may involve removal of a physical impediment to an impaired natural function, such as a constructed shoreline (Warren et al. 2002), or a disturbance, such as fishing, relying on natural recovery. More commonly, however, in habitats dominated by species that create biogenic habitat, rehabilitation includes re-establishing those species (Orth et al. 1994, Van Treeck & Schuhmacher 1999, Hernández-Carmona et al. 2000, Perkol-Finkel & Benayahu 2009), often into novel or newly created habitat.

Intertidal and shallow subtidal rocky habitat has generally been considered resilient to many anthropogenic disturbances (Thompson et al. 2002), in part because numerous natural disturbing forces repeatedly affect intertidal shorelines. Waves or desiccation have major influences on many ecological processes and are considered dominant forces structuring intertidal assemblages (e.g. Dayton 1975, Sousa 1979, Littler et al. 1983, Underwood 1999). Intertidal rocky shores support many species that create habitat for other species at small or large scales, e.g. mussels (Lohse 1993) or canopy algae (Underwood 1998, Benedetti-Cecchi et al. 2001). Disturbances, such as harvesting (Dye 1992), wave action (Dayton 1971) or

storms (Underwood 1998), clear organisms from the rock surface, creating bare patches. These patches are usually small and assemblages recover quickly (Sousa 1979, Underwood 1998). However, some species take longer to recover, even in relatively small patches (e.g. Underwood 1999), and some intertidal disturbances are very large, affecting entire shorelines (Castilla 1988, McCook & Chapman 1993).

Intertidal and shallow subtidal boulder fields are very vulnerable to small- and large-scale disturbances because individual boulders, on and under which many species live, can be moved, buried or overturned for long periods of time (Sousa 1979, Cryer et al. 1987, McGuinness 1987). Abrasion as boulders move kills many species living on the boulders, maintaining an early successional assemblage, especially on wave-exposed coasts (Lieberman et al. 1979). Even on sheltered coasts, many species are killed by occasional events that cause boulders to be buried or overturned (Osman 1977, Sousa 1979, McGuinness 1987). Most species living on the upper surfaces of boulders in relatively sheltered sites also live on rocky shores, but many of those confined to the undersurfaces of boulders are habitat specialists (Kangas & Shepherd 1984, Grayson & Chapman 2004, Chapman 2005). Repeated or prolonged disturbances can have deleterious effects on this fauna, although some mobile species living under boulders can disperse to other boulders when disturbed (Smoothey & Chapman 2007) and most species survive occasional short-term disturbances (Chapman & Underwood 1996).

On urbanized shores, species in intertidal boulder fields are particularly vulnerable to loss and disturbance of habitat and boulder fields have been considered a threatened habitat (Francis et al. 2008). Even though intertidal boulders support many rare species (Chapman 2005, Londoño-Cruz & Tokeshi 2007), there has been little research on these species in urbanized environments, although constructed boulder fields in urbanized harbours do support some fauna (Chapman 2006). Most experimental tests on restoration of boulder habitat have used boulder substitutes in existing boulder fields (McGuinness & Underwood 1986, Chapman 2003b). There have been few experiments at the scale of entire boulder fields, although Chapman (2012) examined the colonization of species onto small patches of new boulders deployed outside nearby natural boulder fields.

As part of a larger study on rehabilitation of boulder fields, Chapman (2012) described colonization to replicate patches of newly quarried sandstone over a range of scales from 10s of metres to kilometres. The

sessile assemblage on these new boulders did not converge with that on natural boulders but was dominated by opportunistic algae. Nevertheless, many mobile animals rapidly colonized these new patches. The resulting assemblage was dominated by molluscs and echinoderms, with extremely patchy distributions among patches and among individual boulders, as is the case for natural boulders (Chapman 2002, 2005). Most variation was at the scale of metres to 10s of metres, rather than kilometres, so it was recommended that multiple small reefs be built over a larger area rather than attempt to find the 'best' place to site one large reef.

There is still, however, a question about whether larger artificial patches attract or support more species than do smaller patches as predicted by species-area theory (MacArthur & Wilson 1967), although McGuinness (1984) and Chapman & Underwood (2009) showed that species–area relationships on intertidal boulders were very variable and not readily predictable. The model of resource concentration also suggests more colonization and greater persistence of species in large patches (Grez & Gonzalez 1995). Results of tests of this theory in marine habitats are contradictory. Several small patches may support different taxa and, hence, more species (McNeill & Fairweather 1993), or large patches may support species that do not occur in any small patch (Oertli et al. 2002). Few such comparisons have been done using artificially created habitat, but artificial habitat may not show patterns that are similar to those of natural patches of habitat (McNeill & Fairweather 1993).

In 2 sites on 1 of the shores described by Chapman (2012), the effect of 2 different patch sizes on colonization was evaluated. In addition to the 3 patches of 50 boulders each (50B patches), 2 replicate patches of 100 boulders (100B patches) were added to each site. Although these were small patches compared to many natural boulder fields, which may have boulders spread over 100s of m² or more, they were similar to the patches of rubble left as debris along urbanized shorelines (Chapman 2006), the boulders deployed at the base of urban infrastructure to disperse wave action (Green et al. 2012) and the sizes of patches that may be deployed in association with marinas to provide habitat (Iversen & Bannerot 1984). It was also not logistically possible to deploy larger reefs because of the limited area available near natural boulder fields. The boulders were used to test the model that these 2 patch sizes create equivalent habitat for mobile animals living on and under boulders and, therefore, that, within these limitations,

patch size is not a major factor determining colonization of newly created habitat. Thus, it was predicted that similar numbers of species and abundances of individual species would colonize 50B and 100B patches. The species colonizing these patches were also compared to those found on large natural boulder fields in the vicinity at greater resolution than described by Chapman (2012).

MATERIALS AND METHODS

Field experiments

Five patches of newly quarried boulders were deployed in each of 2 sites (S1 and S2) at Cape Banks (New South Wales, Australia; as described by Chapman 2012) in December 1999. These sites are ~500 m apart, relatively sheltered, with similar exposure to waves. Each contains a natural boulder field, with a diverse assemblage of invertebrates, particularly molluscs (Chapman 2005). Each patch was deployed low on the shore, with the tops of the new boulders emersed during spring low tides, but the under-surfaces always submersed. The rock type and range of sizes was similar to that of many natural boulders, i.e. a diameter of ~25 to 50 cm. Larger boulders were not included in the present study because it is not possible to sample natural boulders larger than this and also replace them without damage to the animals living under them. Sandstone was used because rock type does affect colonization of boulders (McGuinness & Underwood 1986, James & Underwood 1994) and most boulders in these sites are sandstone. The new boulders were placed randomly but, within a few days, had moved and stabilized, with <1 m between adjacent boulders, irrespective of the number of boulders deployed in each patch. In each site, 2 patches were made with 100 boulders each (100B patches) and 3 patches with 50 boulders (50B patches). There were 10 to 50 m between patches and at least 20 m between these and natural boulders. It was not possible to deploy the patches further from the natural boulders while also ensuring similar depth and surrounding habitat.

Mobile animals on the upper and lower surfaces of the boulders were identified and counted 1, 3, 5, 7, 9, 12, 16, 27, 38 and 52 wk after deployment. Fast-moving species that shelter under boulders, including shrimp, crabs and fish, were not counted. Because the main focus of comparison was the scale of the patches, rather than individual boulders, 10% of each patch was sampled each time, i.e. 5 randomly

selected boulders in the 50B patches and 10 randomly selected boulders in the 100B patches. This maintained the proportion of boulders disturbed at each time of sampling between the 2 patch sizes, so the likelihood of resampling a previously sampled boulder was similar among patches. Previous work (Chapman & Underwood 1996) had shown that resampling boulders had no effect on assemblages living under them, unless the same boulders were repeatedly sampled on consecutive days, as long as the boulders were sampled quickly and replaced in their original position. That procedure was followed here. Sampling was restricted to animals visible to the naked eye (>5 mm in length) which could be sampled *in situ* with minimal disturbance. All echinoderms and molluscs were identified to species, except for the family Columbellidae and small brittle stars because identification needed to be rapid and the boulders replaced before the disturbed animals moved from the boulders (Chapman & Underwood 1996). Fifteen randomly selected natural boulders in the nearby boulder field were sampled once during early colonization (5 wk) and at the last 3 times of sampling (27, 38 and 52 wk). Natural boulders were not sampled at each time because of ongoing sampling and experiments in the natural boulder field and the need to minimize further disturbance.

Analyses of data

At each time of sampling, the 5 boulders in each of 2 randomly selected 50B patches in each site and 5 of the 10 boulders in each 100B patch were selected at random for a balanced design, and the assemblages were compared using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on Bray-Curtis dissimilarities (Clarke et al. 2006) from untransformed data. When the factor of Size (of patch) or the interaction Size × Site was significant, the species that together contributed to 50% of the difference between the 2 patch sizes were identified. Differences between patches and natural boulders, when sampled, were visualized in non-metric multi-dimensional scaling (NMDS) plots of the centroids calculated from the all sampled boulders.

Most taxa were extremely variable among individual boulders. There were many counts of zero, the mean abundances were small and variances were invariably heterogeneous (as is common for these fauna; Chapman 2002, 2005). Similarly, some boulders supported many species, whereas others sampled at the same time supported only 1 or 2

and the identity of the species varied considerably among replicate boulders. Therefore, to compare the number of species on sampled boulders in patches of different sizes (with columbellids and small brittle stars treated as if they were species), the number of species found on all sampled boulders in 50B or on all 100B patches at each time separately were compared after taking into account the different numbers of boulders sampled. At each time, 40 boulders were sampled across the four 100B patches, but only 30 in the six 50B patches. To be able to compare the number of species across similar numbers of boulders in each patch size, 30 of the 40 boulders in the 100B patches were randomly selected and the number of species on these were calculated. This was repeated 100 times for each time of sampling and the mean number of species for the 100 random sets of 30 boulders was calculated. This mean was used as the expected number to be found on 30 boulders, assuming that 30 boulders in six 50B patches is equivalent to 30 boulders from four 100B patches. This mean was then compared to the observed number found on the 30 boulders sampled on the 50B patches at each time using χ^2 tests. This tested the hypothesis that both patch sizes support similar numbers of species given the same sampling intensity. Similarly, samples of 15 of the 40 boulders from 100B patches or of the 30 boulders from 50B patches were compared to the number of species on natural boulders using χ^2 tests to test the hypothesis that boulders in these patches supported the same numbers of species as a similar number of natural boulders.

To compare the abundances of individual species among patches of different sizes, abundances were summed over all 50B and all 100B patches at each time. The distributions of all taxa with >25 individuals at most times of sampling were compared among treatments at each time with the numbers expected in each treatment from the numbers of boulders sampled, assuming the null hypothesis was true (χ^2 tests). For species that were less abundant, data were summed over all times of sampling. Results were only considered significant when p < 0.05 and the expected numbers exceeded 5 for each cell in the analysis.

In addition, to test directly whether more species and more individuals would colonize 2 separate 50B patches compared to one 100B patch, or vice versa, the numbers of species and the number of individuals on each pair of two 50B patches (i.e. 3 such pairs) were compared graphically to those on each 100B patch for each time separately.

RESULTS

Effect of patch size

Most fauna colonizing boulders in the constructed patches were molluscs (chitons, gastropods and opisthobranchs) and echinoderms (sea urchins, starfish, brittle stars and occasional holothurians). Platyhelminths, nemerteans and errant polychaetes were relatively rare, together generally comprising <5% of the assemblage. This assemblage thus broadly resembled that on natural boulders, where the macrofauna is dominated by molluscs and echinoderms (Chapman 2002, 2005).

Comparison of the assemblages using PERM-ANOVA (Anderson 2001) showed that sites never differed significantly and the 2 patch sizes only differed significantly at Weeks 2 and 38 (illustrated for 7 times of sampling in Table 1). At these times, differences between patch sizes were dominated by only a few species. At Week 2, the limpet *Patella mufria*, the gastropods *Cantharidella picturata* and *Austrocochlea porcata* and the Columbellidae together contributed 53% to the dissimilarity between patches of different sizes. At Week 38, 52% of the dissimilarity was due to the sea urchin *Heliocidaris erythrogramma*, the starfish *Patiriella exigua*, the limpets *P. mufria* and *Cellana tramoserica*, the gastropods *Australium tentoriforme*, *Turbo torquatus* and *A. porcata* and the chitons *Ischnochiton australis* and *I. versicolor*. Patterns in the assemblages are illustrated in NMDS plots in Fig. 1 for 2, 12, 38 and 52 wk after the experiment was set up. They show considerable variation among patches, compared to differences between the treatments, even when patch sizes differed significantly in the analyses.

There was also considerable variation in assemblages among boulders within patches; mean dissimilarities among replicate boulders within patches were 71 to 92%. There was no trend for assemblages on individual boulders to become more similar through time and no consistent differences in within-patch variation between 100B and 50B patches (Fig. 2). Similarly, there was no tendency for the different patches within either treatment (i.e. constructed of 50 or 100 boulders) to become more similar through time, although 100B patches were consistently more similar to each other than were 50B patches (Fig. 2).

Between 31 (after 1 wk) and 63 (after 7 wk) taxa of molluscs (all identified to species, except for Columbellidae) and echinoderms (all identified to species, except for small brittle stars) were found in the built
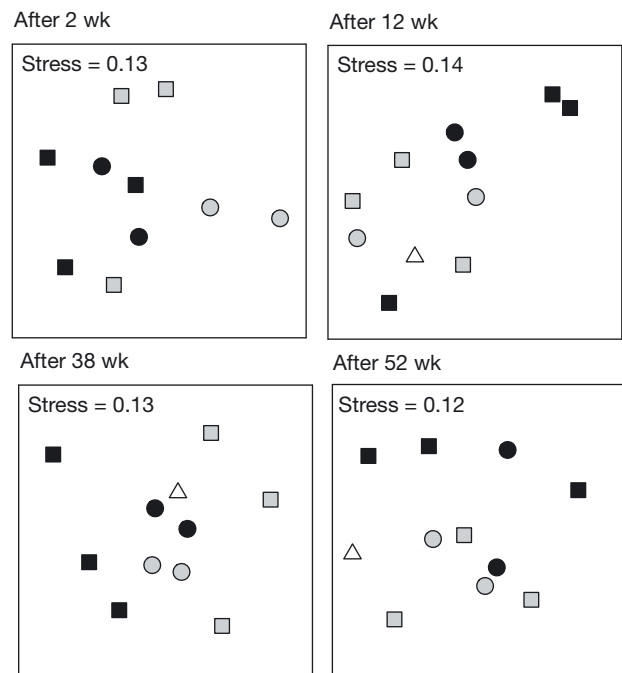

Fig. 1. NMDS plots of assemblages in (●) 100B and (■) 50B patches of boulders in (black and grey symbols) 2 sites after 2, 12, 38 and 52 wk; (△) assemblages on natural boulders; data are centroids from 5 boulders (50B patches), 10 boulders (100B patches) and 15 (natural) boulders

Table 1. Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) of assemblages on 5 randomly selected boulders from each of two 50B and 100B patches of artificial boulders 1, 2, 5, 12, 27, 38 and 52 wk after the patches were created; St: site, random, 2 levels; Sz: size of patch, fixed, 2 levels; P: patches, nested in Size and Site; n = 5; data were not transformed; levels of significance determined from 4999 permutations; *p < 0.05, **p < 0.01

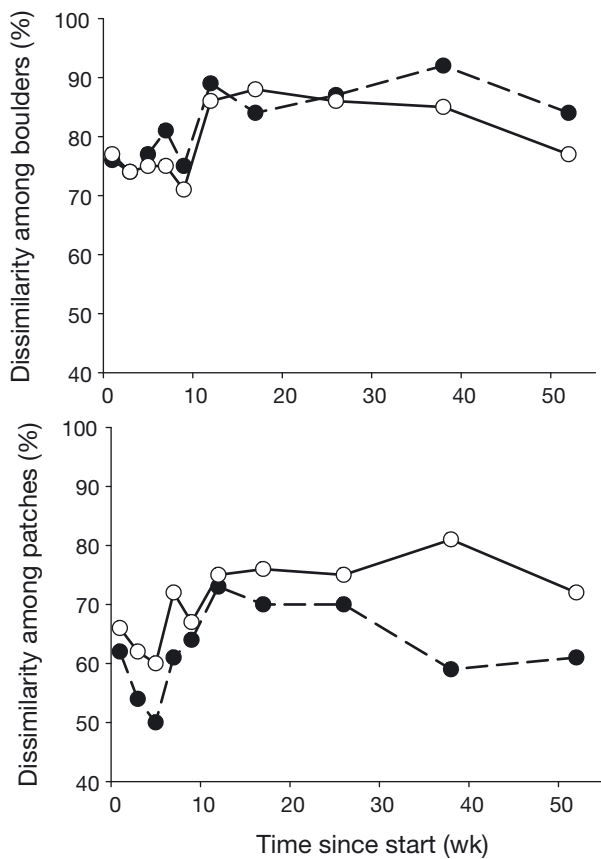| No. of weeks:	1		2		5		12		27		38		52	
	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
St	5182	2.18	3678	0.61	5501	1.60	5248	0.77	7316	1.26	9905	1.94	6846	0.89
Sz	5062	1.17	14777	4.62**	2028	0.67	8068	1.21	4382	0.55	10749	1.78*	7538	0.99
St × Sz	4326	1.82	3197	0.53	3025	0.88	6649	0.97	7889	1.36	6040	1.18	7712	1.01
P(St × Sz)	2375	1.25	6020	2.15**	3436	1.07	6829	1.73**	5790	1.52**	5099	1.32	7645	2.18**
Residual	1904		2794		3201		3945		3800		3882		3498	

Fig. 2. Mean dissimilarity among replicate boulders within patches and among replicate patches (calculated from the centroid of each patch at each time of sampling) for (dashed line) 100B and (solid line) 50B patches from 1 to 52 wk after the start of the experiment

man & Underwood 1996, Chapman 2002, 2005) and the habitat use described in the literature was used to support this division. Species that could not be unambiguously assigned to either category, <5 found per time of sampling, were omitted from these analyses.

There were no general patterns in the relative numbers of generalist or specialist species on 50B or 100B patches at different times of sampling (Table 2). There were, however, more specialist species on the 100B patches than on the 50B patches at 8 of the 10 times of sampling. When the number of species on the 30 boulders in 50B patches was compared to the average number of species on 100 random samples of 30 boulders from 100B patches, there was no significant effect of patch size on the numbers of species found, except for more generalist species on 50B patches than predicted after 16 wk (Table 2). Thus, larger patches had larger numbers of specialist species, due to the fact that more boulders were sampled in the larger patches, but there was no difference in the numbers of species on similar numbers of boulders in each treatment.

Most species living under boulders are sparse (Chapman 2005), and despite sampling 70 boulders each time, the abundances of many taxa were too sparse for analysis. Those that were analysed through time (Table 3) generally showed consistent patterns between the 2 patch sizes from time to time, although these patterns varied among species. Thus, the predatory starfish *Coscinasterias calamara* was generally more abundant in 100B patches than expected by chance, but only after 1 wk was this dif-

patches. These were divided into generalist and specialist species. The generalists are common on intertidal shores and on the substratum around the boulders. They included starfish (e.g. *Patiriella calcar*), sea urchins (e.g. *Heliocidaris erythrogramma*), grazing (e.g. the limpet *Cellana tramoserica*) and predatory (e.g. *Cabastana spengleri*) gastropods and numerous nudibranchs and other opisthobranchs. The specialists included numerous chitons, especially of the genus *Ischnochiton*, limpets such as *Scutus antipodes* and *Amblychilepas nigrita*, abalone (e.g. *Haliotis rubra*) and other grazers, such as *Gena impertusa* and *Granita imbricata*. Long-term studies (e.g. Chap-

Table 2. Number of generalist (Gen.) and specialist (Sp.) species sampled on 40 boulders in the 100B patches, number sampled on 30 boulders in the 50B patches, mean number predicted for 30 boulders from the 100B patches (averaged over 100 random samples) and χ^2 tests on the number of species sampled in 50B patches compared to the number predicted from 30 boulders in 100B patches. *p < 0.05

Week	40 boulders in 100B patches		30 boulders in 50B patches		Mean no. per 30 boulders in 100B patches		χ^2	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
1	12	13	12	6	11.2	12.0	0.06	3.02
3	16	21	19	16	12.5	18.4	3.37	3.31
5	15	22	19	21	14.3	20.1	1.55	0.04
7	26	21	28	18	22.8	18.9	0.46	0.04
9	21	21	22	19	21.2	19.3	0.03	0.00
12	24	20	19	13	21.8	18.9	0.36	1.60
16	17	21	26	16	15.9	19.7	6.35*	0.69
27	18	11	20	14	15.5	15.4	1.33	0.13
38	18	21	20	12	16.1	18.6	0.95	2.31
52	26	19	20	20	23.7	17.1	0.57	0.51

Table 3. Number (n) and percentage (%) of selected species found on 100B patches at each time of sampling or summed over all times; significant variation from chance expectations using χ^2 tests indicated in **bold**; the percentage expected on the 100B patches under the null hypothesis is 57%

| Time since start (wk): | 1 | | 3 | | 5 | | 7 | | 9 | | 12 | | 16 | | 27 | | 38 | | 52 | | All times | |
Species	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Echinoderms																						
Coscinasterias calamara	**14**	**99**	29	55	23	57	42	67	40	60	24	67	21	67	9	100	8	75	5	100		
Patiriella exigua	0	0	9	0	**24**	**12**	**38**	**3**	**52**	**0**	**29**	**0**	**22**	**0**	4	0	**17**	**6**	8	0		
Heliocidaris spp.																					127	64
Ophiuroids																					162	59
Limpets																						
Patella mufria	81	60	**185**	**82**	107	60	**28**	**82**	**50**	**78**	**17**	**94**	9	67	34	59	**19**	**89**	86	66		
Patella alticostata																					117	64
Notoacmea flammea[a]	7	54	16	44	29	62	**90**	**86**	**39**	**90**	4	100	27	67	6	100	**11**	**91**	28	57		
Cellana tramoserica																					**136**	**35**
Amblychilepas nigrita[a]																					24	25
Other gastropods																						
Cantharidella picturata	127	50	**253**	**49**	**189**	**7**8	125	53	**289**	**67**	99	55	15	25	19	75	7	100	54	17		
Austrocochlea porcata	**54**	**33**	47	**0**	36	**0**	61	**0**	54	2	33	3	24	**7**	31	**2**	18	**5**	5	0		
Eurytrochus strangei[a]																					66	55
Turbo torquatus																					**64**	**41**
Australium tentoriforme																					**185**	**79**
Gena impertusa[a]																					**135**	**73**

[a]Species that are predominantly found under boulders in this habitat

ference statistically significant. In contrast, the herbivorous starfish *Patiriella exigua* was consistently found more in 50B patches.

Two species of limpets (*Patella mufria* and *Notoacmea flammea*) were analysed for each time separately (Table 3). Both were generally found more in 100B patches than expected by chance (observed 10 and 7 times, respectively), but differences were not always significant. The 2 trochid gastropods *Cantharidella picturata* and *Austrocochlea porcata* showed different patterns. The former showed no consistent pattern from time to time, being more abundant on 100B patches than expected by chance on 4 occasions but less abundant on 6 occasions (Table 2). *A. porcata*, in contrast, was similar to *P. exigua* and consistently more abundant on 50B patches. The chitons *Ischnochiton australis* and *I. versicolor*, which often co-exist on the same boulders (Grayson & Chapman 2004), also showed variable patterns through time (Table 3), but there was a trend for greater abundances on boulders in 100B patches.

Of the remaining species, data were summed over times, but most species were still too sparse to analyse, although they generally showed patterns which appeared consistent with random distributions between patch sizes. Of those that could be analysed when data were summed over all times of sampling, the limpet *Patella alticostata* and the trochid gastropod *Eurytrochus strangei* similarly showed no sig-

nificant differences in distributions between 50B and 100B patches (Table 3). The sea urchins *Heliocidaris erythrogramma* and *H. tuberculata* (data for both species combined) and ophiuroids (all species combined) were generally more abundant in 100B patches, although differences were not significant (Table 3). The turbinid gastropod *Australium tentoriforme*, the boulder-specialist *Gena impertusa*, and 4 species of chitons were significantly more abundant on 100B patches.

Two other limpets, *Cellana tramoserica* (a widespread inter- and subtidal species) and *Amblychilepas nigrita* (a rare species generally only found under boulders), another turbinid, *Turbo torquatus*, the 2 opisthobranchs *Elysia* sp. and *Austraeolis ornata* and the small chiton *Acanthochiton* sp. were all more common on 50B patches, with significant differences for all species except *A. nigrita*.

To test directly whether more species and more individuals would colonize 2 separate 50B patches compared to one 100B patch, or vice versa, the numbers of species and the number of individuals on each pair of two 50B patches (i.e. 3 such pairs) were compared to those on each 100B patch for each time separately. This was done for all species and, separately, for those species predominantly found under boulders (the boulder specialists). Similar patterns were found for each set of species, whether numbers of species or numbers of animals was considered. In

Site 1, there were generally more species and more individuals on each 100B patch than on the all pairs of 50B patches, especially after 7 wk. This is illustrated for the numbers of all species and the abundances of boulder specialists in Fig. 3. In Site 2, pairs of 50B patches generally had more species and more animals than the 100B patches, although the differences were not large (Fig. 3).

Constructed patches versus natural boulders

Because of the design of sampling, the assemblage on natural boulders was not compared statistically with the constructed patches because there were different numbers of replicates and the natural boulders did not occur in discrete patches. The NMDS plots did not, however, indicate that the differences between assemblages on the constructed patches and the natural boulders were larger than the differences among different patches of constructed boul-

ders (Fig. 1). Similarly, mean Bray-Curtis dissimilarities calculated between the centroids of the 50B or 100B patches and of the sampled natural boulders after 5, 27, 38 and 52 wk (Fig. 4) showed no major differences between artificial and natural boulders. Dissimilarities between the 100B and 50B patches and between each of these patches and the natural boulders were approximately the same as among individual boulders within patches and among replicate patches of the same size (Fig. 4). Up to Week 27, the assemblages on 100B patches differed from those on 50B patches to the same degree as did natural boulders, suggesting that assemblages on 100B patches may have been more similar to natural assemblages than were 50B patches. There were no consistent trends for either size of patch to become more similar to natural boulders over time.

When corrected for different numbers of boulders sampled per treatment, there was no significant difference in the number of species sampled on the 15 natural boulders and the mean number of species on
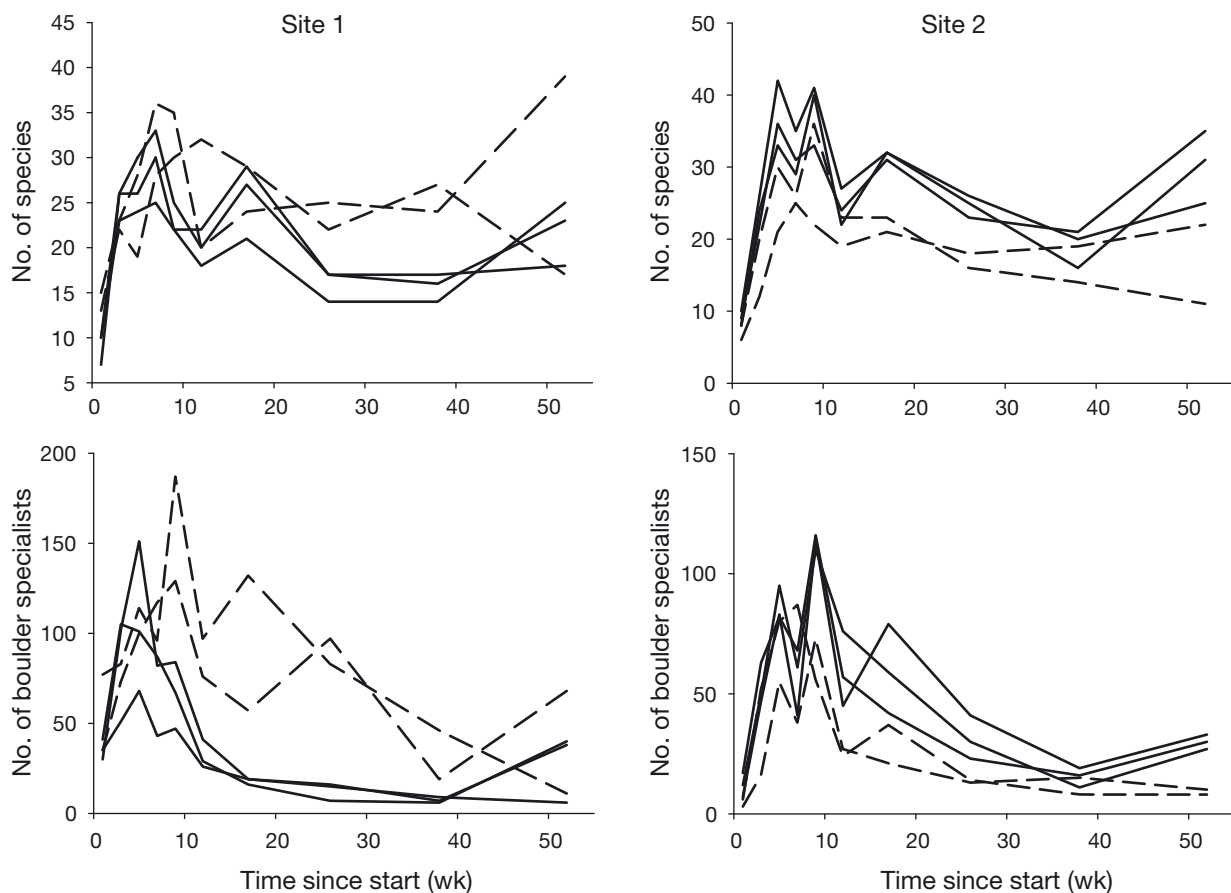

Fig. 3. Total number of all species and total abundances of all boulder specialists on 10 sampled boulders in Sites 1 and 2 for (dashed lines) each 100B patch and for (solid lines) all pairs of 50B patches (5 boulders sampled per patch) from 1 to 52 wk after the start of the experiment
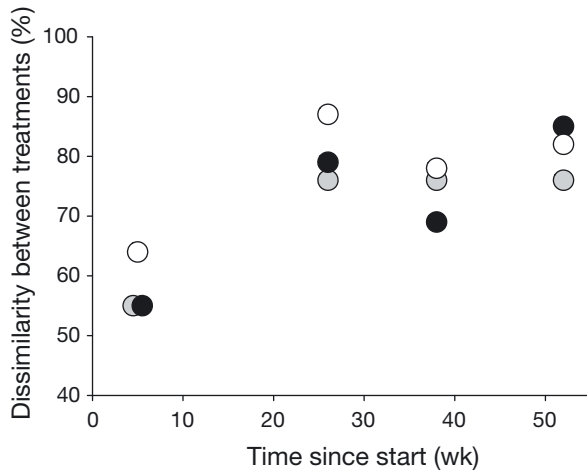
Fig. 4. Mean dissimilarity between (grey) 50B and 100B patches, (white) 50B and natural boulders and (black) 100B and natural boulders (calculated from the centroid of type) for 5, 27, 38 and 52 wk after the start of the experiment

100 random subsets of 15 boulders from the 50B patches at any time (Table 4). Nevertheless, there were generally fewer generalists and specialists on 15 boulders from the 50B patches than on 15 natural boulders except for the last week of sampling. After 5 and 27 wk of deployment, there were significantly fewer generalists on 15 boulders in the 100B patches than on natural boulders (Table 4). This was not the case for specialists or at other times of sampling.

Table 4. Number of generalist (Gen.) and specialist (Sp.) species sampled (a) on 40 boulders in the 100B patches or (b) on 30 boulders in the 50B patches and on the 15 natural boulders, mean number predicted for 15 boulders from the 100B patches or 50B patches (averaged over 100 random samples) and χ^2 tests on the number of species sampled on natural boulders compared to the number predicted from 15 boulders in 100B or 50B patches; *p < 0.05, **p < 0.01

a) Week	40 boulders in 100B patches		15 natural boulders		Mean no. per 15 boulders in 100B patches		χ^2	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
3	12	13	24	21	11.5	15.6	7.85**	1.91
27	18	11	19	12	10.9	12.3	6.10*	0.01
38	18	21	17	8	12.0	13.0	2.09	1.94
52	26	19	11	10	18.0	12.1	2.74	0.35
b) Week	30 boulders in 50B patches		15 natural boulders		Mean no. per 15 boulders in 50B patches		χ^2	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
3	12	6	24	21	17.4	15.8	2.47	1.69
27	20	14	19	12	14.1	9.2	1.69	0.82
38	20	12	17	8	14.9	8.1	0.29	0.00
52	20	20	11	10	17.0	15.6	2.10	1.99

The abundances of each species on the 50B patches or 100B patches were compared to the abundances on the natural boulders, with the data summed for each of Weeks 3, 8, 9 and 10 (when natural boulders were sampled) and compared among treatments to the numbers expected according to the numbers of boulders sampled, assuming the null hypothesis to be true. In contrast to the distributions between the 50B and 100B patches, more results were significant (Table 5), with only 2 grazing gastropods, an elysian opisthobranch and 4 species of chitons showing random distributions among the 3 treatments.

Patterns were not, however, consistent among the other species. The limpets *Patella mufria*, *P. alticostata*, *Notoacmea flammea* and *Scutus antipodes*, gastropods of the genus *Clanculus* and the chiton *Ischnochiton fructicosus* were all more abundant on natural boulders and less abundant on constructed patches than expected by chance. Other species — the starfish *Coscinasteria calamara*, the urchins *Heliocidaris* spp., ophiuroids, the gastropods *Cantharidella picturata*, *Gena impertusa*, *Australium tentoriforme* and *Turbo torquatus*, the nudibranch *Austraeolis ornata* and the chitons *Acanthochiton* spp., *Cryptoplax mystica* and *I. smaragdinus* — were more common on one or both of the sizes of constructed patches than expected. The remaining species were less common on one of the patch sizes but more common on the other patch size and on natural boulders (Table 5).

There were thus no consistent patterns for most species to be more common on 50B patches, 100B patches or natural boulders, although limpets tended to be more common on natural boulders. More importantly, there was no evidence that habitat specialists, i.e. those species only or predominantly found under boulders, were not using the constructed patches in a similar manner to that of the more common and widespread species.

DISCUSSION

Intertidal boulder fields are subjected to many disturbances, causing boulders to move, overturn or be buried (e.g. Sousa 1979, McGuinness

Table 5. Total number and percentages found on 50B and 100B patches and on natural boulders of selected species summed over sampling times 3, 8, 9 and 10; significant variation from chance expectations using χ^2 tests indicated in **bold**; the percentages expected for 50B, 100B patches and natural boulders under the null hypothesis are 35, 47 and 18%, respectively. *p < 0.05, **p < 0.01, ***p < 0.001

Species	Total no.	50B (%)	100B (%)	Natural (%)	χ^2
Echinoderms					
Coscinasterias calamara	43	28	65	7	6.41*
Patiriella exigua	107	45	5	50	**108.93***
Heliocidaris spp.	106	41	45	14	1.64
Ophiuroids	63	43	52	5	7.32*
Limpets					
Patella mufria	285	13	32	55	**285.41***
Patella alticostata	49	20	31	49	**33.10***
Notoacmean flammea[a]	115	17	32	51	**90.72***
Cellana tramoserica	83	58	10	33	**47.06***
Scutus antipodes[a]	26	19	4	77	**63.99***
Other gastropods					
Cantharidella picturata	419	46	42	12	**22.98**
Austrocochlea porcata	212	38	1	61	**325.30***
Eurytrochus strangei[a]	41	49	24	27	8.54*
Clanculus spp.[a]	47	15	13	72	**96.96***
Gena impertusa[a]	36	56	39	6	7.68*
Australium tentoriformis	101	39	48	14	1.14
Turbo torquatus	30	37	50	17	0.38
Opisthobranchs					
Austraeolis ornata[a]	24	8	75	17	8.94*
Elysia sp.[a]	18	50	33	17	1.83
Chitons					
Acanthochiton sp.	43	65	26	9	**16.74***
Cryptoplax mystica[a]	62	37	53	10	2.78
Onithochiton quercinus	29	14	62	24	5.87*
Ischnochiton australis[a]	291	19	54	27	**39.98***
Ischnochiton elongatus[a]	86	19	48	34	**19.38***
Ischnochiton fructicosus[a]	42	31	31	38	**12.49**
Ischnochiton smaragdinus[a]	28	32	57	11	1.46
Ischnochiton versicolor[a]	130	25	48	26	9.00*

[a]Species that are predominantly found under boulders in this habitat

1987). The mobile invertebrates that live under intertidal boulders include many species that are habitat specialists (Chapman 2005). Some tolerate certain levels of disturbance by rapidly redistributing themselves on the disturbed boulders (author's pers. obs.) or by dispersing to nearby boulders (Smoothey & Chapman 2007), although when boulder fields are spaced far apart, adult animals are unlikely to be able to move to a new boulder field when disturbed. Assemblages differ considerably from one boulder field to another, even between those in close proximity, or among sites within a single boulder field, particularly with respect to the rarer fauna (Chapman 2005, Chapman et al. 2009). Chapman et al. (2009) showed different levels of endemism of rare species among boulder fields only a few kilometres apart,

which makes it necessary to decide *a priori* which species to conserve before one can decide which area to protect. The paucity of knowledge for determining risk in marine invertebrates (Chapman 1999) makes this a difficult decision, but a method of making such a choice is described by Chapman et al. (2009).

Major changes to shorelines associated with urbanization, which can cause loss or severe degradation of boulder fields (Francis et al. 2008), may put vulnerable assemblages at risk. Although many marine habitats (e.g. mudflats, saltmarshes and oyster reefs) can be rehabilitated by creating new habitat, which is then naturally colonized, there has been little research on restoration of rocky habitat. Most relevant studies on boulder fields have examined how species colonize novel habitat (e.g. concrete blocks or quarried stones) added to existing boulder fields, rather than to newly created boulder fields. Yet artificially created patches of boulders have been suggested as replacement for destroyed habitat (Iversen & Bannerot 1984), and boulders have been added to streams to create new habitat for fish (Gørtz 1998).

The present experiment examined colonization of patches of newly quarried boulders deployed outside natural boulder fields, but on shores where natural boulder fields occur, to evaluate their value in creating habitat for invertebrate boulder specialists. Although the sessile assemblage developed slowly on these boulders and remained at an early successional state, composed primarily of ephemeral green turfing algae and encrusting tubeworms, the quarried boulders were rapidly colonized by a diverse suite of mobile macrofauna. The assemblage was dominated by echinoderms and molluscs, as are natural boulders on this shore (Chapman 2005, 2012) and included common, widespread species and many of the rare boulder specialists that naturally occur nearby.

It was originally thought that many species, especially the habitat specialists, would colonize these artificial patches as recruits because there was at least 10 m between these patches and the natural

boulder field. In fact, many species, both common, widespread species and species considered as habitat specialists because they are absent or very rare from other intertidal habitats, colonized these patches within a few weeks as adults. Many of the more mobile species, such as the starfish, sea urchins and many gastropods, could have moved over the substratum, which was a patchy matrix of rocky habitat and patches of sediment. Species such as *Turbo* spp., *Austrocochlea porcata* and *Thais orbita* are common on the substratum among boulders. Nevertheless, many specialist species, such as *Ischnochiton* spp., *Cryptoplax mystica*, *Gena impertusa* or *Clanculus* spp. also rapidly colonized these boulders as adults. It is not known how these species dispersed to these patches. Although many of these species are not observed on the substratum around the boulders during the day, they may move out from under boulders to feed at night (Kangas & Shepherd 1984), as has been observed for *Ischnochiton* spp. (J. Grayson pers. comm.). When boulders are disturbed and overturned, many species also drop from the substratum and are moved via the water column (author's pers. obs.). As long as they remain in the boulder field, they can rapidly colonize new boulders when they drop to the bottom. Whether these species use this mechanism as a common means of dispersal among boulders has not yet been observed. Similarly, invertebrates moved into new gravel beds that were placed in rivers to enhance fish habitat by moving in from surrounding habitat (Gørtz 1998).

Most of the variation in abundances and diversity was at the scale of individual boulders (~1 m apart) or among replicate patches of boulders, rather than at scales of 100s of m or more, which is a common feature of these assemblages (Chapman 2002, 2005). Differences in abundances among boulders are often independent of boulder size (Lieberman et al. 1979, Chapman 2005), but not in all studies (Sousa 1979). This variation could be stochastic or influenced by the identity of early colonizers. Similar small-scale variation in abundances is also common for species living on boulders in rivers, with most variation at the scale of individual boulders or riffles (Downes et al. 1993, 1995). It has thus been proposed that, in the absence of further knowledge on cues to which these intertidal species respond, it would be less risky to create new boulder habitat in multiple small-scale patches than to create a single larger patch of boulders. All else being equal, one might, however, expect boulders in larger patches to be colonized at a faster rate than those in smaller patches because the 100B patches had both a larger area and a longer perimeter. This should increase colonization from settling larvae in the water column and from adults moving from the surrounds (Hanski 1991). In addition, the model of resource concentration suggests that there may be more resources in larger patches (Grez & Gonzalez 1995).

Over the scales tested here, similar numbers of species colonized the same number of boulders in the different patch sizes, with only the generalist species showing a significant effect of patch size at one time of sampling. In addition, most taxa showed no difference in abundances between patches of different size. Therefore, there was no evidence that most of the species distinguished between 100B and 50B patches. Those species that did show a significant difference in abundance between the 2 patch sizes included echinoderms and molluscs. Although some species showed quite strong patterns, there was no generality in these patterns. Thus, some species were more abundant on 50B patches, whereas other related species showed the opposite pattern. Studies comparing the numbers of species/abundances on numerous small boulders relative to fewer large boulders (Douglas & Lake 1994, Londoño-Cruz & Tokeshi 2007) have also given different results for different species.

Because there was no evidence that boulders in 50B patches differed fundamentally from 100B patches, together with the fact that there was considerable variation in abundances at the scale of patches, it was proposed that two 50B patches might support more species or individuals than one 100B patch because, although covering a similar area, the greater spatial separation in two 50B patches might capture greater environmental variability. This was supported in one of the sites for both the number of taxa and the number of animals and for all species and the rarer species. In the other site, however, both 100B patches supported more species/individuals than all combinations of two 50B patches. When compared to natural boulders, there were some statistically significant patterns, but many species — including common and rare species of molluscs and echinoderms — were as or more abundant on the constructed patches than on the natural boulders. There was no tendency for 50B or 100B patches to be more or less similar to natural boulders or to show greater convergence with natural habitat through time. This variation in response probably reflects the large amount of small-scale variability in these fauna (Chapman 2005).

Thus, there is evidence that newly quarried stones can be successfully used to create suitable boulder

habitat in that numbers of both generalist and specialist species converged with those on samples of natural boulders within a few months. Numerous small patches of boulders, perhaps of differing sizes, spread over a large area of shore may be the best strategy to create new boulder fields in disturbed environments because small patches of quarried boulders do serve as habitat for most species and this strategy involves spreading the risk (den Boer 1968). This is relatively cheap and easy, compared to rehabilitating or recreating many marine habitats or finding a suitable site for one large boulder field in a highly disturbed and altered environment. Because both larvae and adults recruited to this novel habitat very readily, colonization should be rapid, although for adult recruitment, there must be a nearby source of colonists. Dispersal among boulders by many of these rarer species has not yet been studied in enough detail to understand where these colonists come from, but some species move off boulders to forage at night (e.g. Smoothey & Chapman 2007) and possibly move great distances. Other species drop from disturbed boulders and are washed by water movement to adjacent suitable habitat (author's pers. obs.). Whether this is a common mode of movement in undisturbed habitat is not known. Because colonization is rapid, the newly created habitat does not need to be pre-conditioned in any way before the animals respond to it.

Deploying patches of artificial habitat near natural undisturbed boulder fields is therefore likely to speed up colonization because adult animals can move into these new habitats. They are therefore not totally dependent on larval recruitment. Isolation from nearby populations of animals will reduce rates of colonization, most particularly for habitat specialists. There must at this stage, however, be concern about attracting animals from a natural habitat to what might in the long term be sub-optimal habitat. There is a need for longer term studies to identify the relative importance of larval recruitment and adult immigration and the rates at which habitat generalists and specialists will colonize new habitat. Only then can the role of created habitat in the production of new populations, in contrast to the attraction of individuals from existing populations, be elucidated.

With coastal squeeze from urbanization, potential sea level rise and increased storm intensity, intertidal boulder fields and their specialist biota are threatened. The rarer species may be those most at risk (Walker et al. 2008). The present work suggests that intertidal boulder fields can be restored or built anew, thus meeting some of the 'challenges of urban

river habitat restoration' (Francis et al. 2008). Although encouraging, these results do not demonstrate that these replicate patches of quarried boulders can replace natural boulder fields. More studies are essential before one can be complacent about the long-term sustainability of these habitats. Nor is it proposed that such patches should be built in mitigation for the destruction of natural habitat. In highly altered and urbanized landscapes, however, where much natural habitat has already been lost, the introduction of quarried boulders is a form of ecological engineering (Chapman & Underwood 2011) that may assist in the protection of many rare species.

LITERATURE CITED

Able KW, Manderson JP, Studholme AL (1998) The distribution of shallow water juvenile fishes in an urban estuary: the effects of manmade structures in the lower Hudson River. Estuaries 21:731–744

Airoldi L, Beck MW (2007) Loss, status and trends for coastal habitats of Europe. Oceanogr Mar Biol Annu Rev 45: 345–405

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150

Bilkovic DM, Roggero M, Hershner CH, Havens KH (2006) Influence of land use on macrobenthic communities in nearshore estuarine habitats. Estuaries Coasts 29: 1185–1195

Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. J Appl Ecol 47:26–35

Burdick DM, Short FT (1999) The effects of boat docks on eelgrass beds in coastal waters of Massachusetts. Environ Manag 23:231–240

Castilla JC (1988) Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. Science 242:440–443

Chapman MG (1999) Are there adequate data to assess how well theories of rarity apply to marine invertebrates? Biodivers Conserv 8:1295–1318

Chapman MG (2002) Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. Austral Ecol 27:211–228

Chapman MG (2003a) Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Mar Ecol Prog Ser 264:21–29

Chapman MG (2003b) The use of sandstone blocks to test hypotheses about colonization of intertidal boulders. J Mar Biol Assoc UK 83:415–423

Chapman MG (2005) Molluscs and echinoderms under boulders: tests of generality of patterns of occurrence. J Exp Mar Biol Ecol 325:65–83

Chapman MG (2006) Intertidal seawalls as habitats for molluscs. J Molluscan Stud 72:247–257

Chapman MG (2012) Restoring intertidal boulder-fields as habitat for 'specialist' and 'generalist' animals. Restor Ecol 20:277–285

Chapman MG, Underwood AJ (1996) Experiments on effects of sampling on biota under intertidal and shallow subtidal boulders. J Exp Mar Biol Ecol 207:103–126

Chapman MG, Underwood AJ (2009) Evaluating accuracy and precision of species-area relationships for multiple estimators and different marine assemblages. Ecology 90:754–766

Chapman MG, Underwood AJ (2011) Evaluation of ecological engineering of 'armoured' shorelines to improve their value as habitat. J Exp Mar Biol Ecol 400:302–311

Chapman MG, Underwood AJ, Clarke KR (2009) New indices for ranking conservation sites using relative 'endemism'. Biol Conserv 142:3154–3162

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. J Exp Mar Biol Ecol 330:55–80

Clynick BG (2006) Assemblages of fish associated with coastal marinas in north-western Italy. J Mar Biol Assoc UK 86:847–852

Cryer M, Whittle GN, Williams R (1987) The impact of bait collection by anglers on marine intertidal invertebrates. Biol Conserv 42:83–93

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41:351–389

Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol Monogr 45:137–159

Dearborn DC, Kark S (2010) Motivations for conserving urban biodiversity. Conserv Biol 24:432–440

den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheor 18:165–194

Douglas M, Lake PS (1994) Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. Oikos 69:387–396

Downes BJ, Lake PS, Schreiber ESG (1993) Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. Freshw Biol 30:119–132

Downes BJ, Lake PS, Schreiber ESG (1995) Habitat structure and invertebrate assemblages on stream stones — a multivariate view from the riffle. Aust J Ecol 20:502–514

Dye AH (1992) Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish harvesting. Neth J Sea Res 30:209–217

Epstein N, Bak RPM, Rinkevich B (2003) Applying forest restoration principles to coral reef rehabilitation. Aquat Conserv 13:387–395

Erdle SY, Davis JLD, Sellner KG (2006) Management, policy, science, and engineering of nonstructural erosion control in the Chesapeake Bay. In: Erdle SY, Davis JLD, Sellner KG (eds) Proc 2006 Living Shoreline Summit. Chesap Res Consort Publ No. 08-164

Field CD (1999) Rehabilitation of mangrove ecosystems: an overview. Mar Pollut Bull 37:383–392

Francis RA, Hoggart SPG, Gurnell AM, Coode C (2008) Meeting the challenges of urban river habitat restoration: developing a methodology for the River Thames through central London. Area 40:435–445

Glasby TM (1999) Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. Mar Ecol Prog Ser 190:113–124

Gørtz P (1998) Effects of stream restoration on the macroinvertebrate community in the River Esrom, Denmark. Aquat Conserv 8:115–130

Grayson JE, Chapman MG (2004) Patterns of distribution and abundance of chitons of the genus *Ischnochiton* in intertidal boulder fields. Austral Ecol 29:363–373

Green DS, Chapman MG, Blockley DJ (2012) The ecological consequences of the type of rock used in the construction of artificial boulder-fields. Ecol Eng 46:1–10

Grez AA, Gonzalez RH (1995) Resource concentration hypothesis: effect of host plant patch size on density of herbivorous insects. Oecologia 103:471–474

Hanski I (1991) Single-species metapopulation dynamics: concepts, models and observations. Biol J Linn Soc 42:17–38

Hernández-Carmona G, García O, Robledo D, Foster MS (2000) Restoration techniques for *Macrocystis pyrifera* (Phaeophyceae) populations at the southern limit of their distribution in México. Bot Mar 43:273–284

Hobbs RJ, Arico S, Aronson J, Baron JS and others (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeogr 15:1–7

Holloway MG, Connell SD (2002) Why do floating structures create novel habitats for subtidal epibiota? Mar Ecol Prog Ser 235:43–52

Iversen ES, Bannerot SP (1984) Artificial reefs under marine docks in southern Florida. N Am J Fish Manag 4:294–299

James RL, Underwood AJ (1994) Influence of colour of substratum on recruitment of spirorbid tubeworms to different types of intertidal boulders. J Exp Mar Biol Ecol 181:105–115

Kangas M, Shepherd SA (1984) Distribution and feeding of chitons in a boulder habitat at West Island, South Australia. J Malacol Soc Aust 6:101–111

Lieberman M, John DM, Lieberman D (1979) Ecology of subtidal algae on seasonally devastated cobble substrates off Ghana. Ecology 60:1151–1161

Littler MM, Martz DR, Littler DS (1983) Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Mar Ecol Prog Ser 11:129–139

Lohse DP (1993) The importance of secondary substratum in a rocky intertidal community. J Exp Mar Biol Ecol 166:1–17

Londoño-Cruz E, Tokeshi M (2007) Testing scale variance in species-area and abundance-area relationships in a local assemblage: an example from a subtropical boulder shore. Popul Ecol 49:275–285

Luck GW (2007) The review of the relationships between human population density and biodiversity. Biol Rev Camb Philos Soc 82:607–645

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

McCook LJ, Chapman AOR (1993) Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. Mar Biol 115:565–575

McGuinness KA (1984) Species-area relations of communities on intertidal boulders: testing the null hypothesis. J Biogeogr 11:439–456

McGuinness KA (1987) Disturbance and organisms on boulders. II. Causes of patterns in diversity and abundance. Oecologia 71:420–430

McGuinness KA, Underwood AJ (1986) Habitat structure and the nature of communities on intertidal boulders. J Exp Mar Biol Ecol 104:97–123

McNeill SE, Fairweather PG (1993) Single large or several small marine reserves? An experimental approach with seagrass fauna. J Biogeogr 20:429–440

Miller JR, Hobbs RJ (2002) Conservation where people live and work. Conserv Biol 16:330–337

Mitsch WJ, Jørgensen SE (2004) Ecological engineering and ecosystem restoration. John Wiley & Sons, Hoboken, NJ

Oertli B, Joye DA, Castella E, Juge R, Cambin D, Lachavanne JB (2002) Does size matter? The relationship between pond area and biodiversity. Biol Conserv 104: 59–70

Orth RJ, Heck KL, Tunbridge DJ (2002) Predation on seeds of the seagrass *Posidonia australis* in Western Australia. Mar Ecol Prog Ser 244:81–88

Osman RW (1977) The establishment and development of a marine epifaunal community. Ecol Monogr 47:37–63

Perkol-Finkel S, Benayahu Y (2009) The role of differential survival patterns in shaping coral communities on neighbouring artificial and natural reefs. J Exp Mar Biol Ecol 369:1–7

Pranovi F, Curiel D, Rismondo A, Marzocchi M, Scattolin M (2000) Variations of the macrobenthic community in a seagrass transplanted area of the Lagoon of Venice. Sci Mar 64:303–310

Rodney WS, Paynter KT (2006) Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. J Exp Mar Biol Ecol 335:39–51

Rosenzweig ML (2003) Reconciliation ecology and the future of species diversity. Oryx 37:194–205

Russell G, Hawkins SJ, Evans LC, Jones HD, Holmes GD (1983) Restoration of a disused dock basin as a habitat for marine benthos and fish. J Appl Ecol 20:43–58

Seaman W (2007) Artificial habitats and the restoration of degraded marine ecosystems and fisheries. Hydrobiologia 580:143–155

Smoothey AF, Chapman MG (2007) Small-scale variability in the dispersion of the sea urchin *Heliocidaris erythrogramma* among boulders. Mar Ecol Prog Ser 340:89–99

Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol Monogr 49:227–254

Thompson RC, Crowe TP, Hawkins SJ (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environ Conserv 29:168–191

Underwood AJ (1998) Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. J Exp Mar Biol Ecol 231: 291–306

Underwood AJ (1999) History and recruitment in the structure of intertidal assemblages on rocky shores: an introduction to problems for interpretation of natural change. In: Whitfield MJ, Matthews C (eds) Aquatic life cycle strategies: survival in a variable environment. Marine Biological Association of the UK, London, p 79–95

Van Treeck P, Schuhmacher H (1999) Artificial reefs created by electrolysis and coral transplantation: an approach ensuring the compatibility of environmental protection and diving tourism. Estuar Coast Shelf Sci 49:75–81

Walker SJ, Degnan BM, Hooper JNA, Skilleter GA (2008) Will increased storm disturbance affect the biodiversity of intertidal, nonscleratinian sessile fauna on coral reefs? Glob Change Biol 14:1–16

Warren RS, Fell PE, Rozsa R, Hunter Brawley A and others (2002) Salt marsh restoration in Connecticut: 20 years of science and management. Restor Ecol 10:497–513

Zedler JB (1996) Ecological issues in wetland mitigation: an introduction to the forum. Ecol Appl 6:33–37