

Cryptic invertebrates on subtidal rocky reefs vary with microhabitat structure and protection from fishing

Timothy J. Alexander*

Institute of Marine and Antarctic Studies, University of Tasmania, GPO Box 252, Private Bag 49, Hobart, Tasmania 7001, Australia

ABSTRACT: The deployment of flat concrete blocks on subtidal rocky reefs can replicate natural reef microhabitats and provides a means for standardized sampling of cryptic invertebrates. The shape of the cavity beneath the block is related to reef topography and may influence the invertebrate community by affecting the amount of space for cryptic fauna to colonise and influencing the effectiveness of their predator-defence mechanisms. To determine the effect of sub-block reef structure and different levels of external predators on cryptic molluscs and echinoderms, I deployed concrete blocks at locations inside and outside the Maria Island marine reserve in eastern Tasmania, Australia. Relationships between sub-block reef structure and the cryptic invertebrate assemblage were evident between locations, whereas only a small but significant proportion of variation of assemblages between blocks within location was explained by reef surface area. No clear association with external predation pressure was evident in multivariate analyses of variation in assemblage structure. Juvenile abalone *Haliotis rubra* were not influenced by microhabitat structure but were significantly less abundant at protected locations, the only species to exhibit such a response. This result follows a decline of emergent adult abalone in the marine reserve and raises the possibility of recruitment failure of abalone at some fully protected locations in the longer term.

KEY WORDS: Cryptic species · Marine reserve · Abalone · Boulders · Echinoderms · Molluscs

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Benthic cryptofauna represent a poorly sampled but trophically important (Metcalf et al. 2008) functional group of small species that live on subtidal rocky reefs in microhabitats difficult for both predators and researchers to access. These small animals live amongst the cracks, crevices and ledges of bedrock as well as between and beneath loose reef objects such as boulders, cobbles or fractured bedrock sections. Benthic cryptofauna are rarely considered in biodiversity surveys, presumably because they are, by definition, hidden from view and difficult to locate without damaging the substratum. Regardless, this component of the benthic invertebrate assemblage contains both ecologically and commercially valuable species including juvenile sea urchins

(Hereu et al. 2005), abalone (Shepherd 1986), brittle stars (Drolet et al. 2004) and shrimp (Caillaux & Stotz 2003). A prevailing paradigm suggests that individuals are offered protection from predation and adverse environmental conditions by associating with reef features that allow crypsis (e.g. Drolet et al. 2004).

Boulder fields, through their fragmented nature, contain more space for cryptic fauna to colonise than consolidated bedrock habitats, both on the exposed surface layer of boulders (Barry & Wickins 1992) and in the layers beneath (Le Hir & Hily 2005). Intertidal boulder shores have received considerable research attention through the exploration of hypotheses relating to disturbance regimes (Sousa 1979, McGuinness 1987a,b, Smith & Otway 1997), species-area relationships (McGuinness 1984, Smith & Otway 1997, Londoño-Cruz & Tokeshi 2007) and factors affecting

*Email: tjalexander001@gmail.com

temporal and spatial variability in invertebrate taxa (Chapman 2002a,b, Grayson & Chapman 2004, Chapman 2005, Moreira et al. 2007). The benthic cryptofauna of subtidal reefs has received much less attention than their intertidal counterparts. While destructive sampling appears to be the best option for studying benthic cryptofauna in deeper waters (Barnes 2008, Griffiths et al. 2008), the flexibility of SCUBA allows more creative approaches, such as the use of mesh trays of coral rubble to create a standardized habitat area (Takada et al. 2007). Chapman (2003) found invertebrate assemblages that developed under artificially placed, uniformly sized sandstone blocks were similar to those under naturally occurring boulders on the same rocky intertidal shore. This finding suggests that experimentally-placed blocks with standardized area can provide a useful tool when sampling cryptic invertebrates, including in studies that test hypotheses relating to causative mechanisms behind spatial patterns. Confounding effects are not, however, completely eliminated when sampling blocks are used on topographically complex substrata. In these environments, the space available for cryptic fauna to colonise under the block will vary with the rugosity of the reef surface, a potential source of error that may contribute to faunal patterns more than variation associated with the hypothesis under test.

The subtidal benthic habitats of the east coast of Tasmania, Australia, support a diverse cryptic invertebrate assemblage, including juveniles of the state's most valuable fishery species, the blacklip abalone *Haliotis rubra*. My work focused around the long-standing 'no-take' Maria Island marine reserve (declared in 1991), where the numbers of carnivorous fish species bastard trumpeter *Latridopsis forsteri*, blue throat wrasse *Notolabrus tetricus* and the biomass of the dominant benthic predator, the southern rock lobster *Jasus edwardsii*, have greatly increased in response to protection from fishing (Edgar & Barrett 1999, Barrett et al. 2009). The increase in predator biomass, particularly rock lobsters, is thought to be the main contributor to the observation of a steady decline in the abundance of mid-size (30 to 130 mm) blacklip abalone inside the marine reserve (Barrett et al. 2009, Babcock et al. 2010). The free-spawning strategy of *H. rubra* (release of sperm and eggs into the water) means that the probability of successful fertilisation depends on the local density of mature adults (Babcock & Keesing 2000). When the need for spawning in close proximity to a mate is combined with localised dispersal of larvae (McShane et al. 1988), it creates the potential for recruitment failure

in the marine reserve should adult densities continue to decline.

I used concrete blocks as artificial boulders to investigate the benthic cryptofaunal communities of subtidal rocky reefs; specifically to quantify temporal and spatial patterns, and the influence of the sub-block reef structure. By studying locations evenly distributed inside and outside the Maria Island marine reserve, I aimed to explore the influence of increased predator biomass on common cryptofaunal species, establish the presence of newly recruited abalone in the reserve and determine whether the density of cryptic abalone are lower at protected locations in correspondence with the reported patterns in emergent adult populations.

MATERIALS AND METHODS

Survey methods

Five concrete garden pavers (300 × 300 × 50 mm — hereafter referred to as blocks) were haphazardly deployed amongst available near-horizontal positions 1 to 3 m apart at 2 sites separated by 50 m, at each of 12 locations distributed throughout Mercury Passage (Fig. 1). Of the investigated locations, 6 were within the Maria Island Marine Reserve, while the remaining 6 were distributed adjacent to the marine reserve on the west coast of Maria Island and on the coast of mainland Tasmania. Blocks were pre-conditioned at the sites for 6 mo, after which mobile invertebrates were removed and they were scraped free of large algae and sessile invertebrates. The blocks were then deployed for 3 intervals of 3 mo, retrieved in January, April and July 2007 (corresponding to austral summer, autumn and winter respectively; Fig. 2a,b). The abundances of mollusc and echinoderm species were surveyed on the undersurface of the block (Fig. 2c) and on the reef in the footprint of the block. The length of any *Haliotis rubra* was measured to the nearest millimetre using vernier calipers. Fishes (mainly Scorpaenidae, Clinidae) and crustaceans (primarily Paguridae, Alpheidae, Rynchocinetidae) were occasionally observed under the blocks but were excluded from the study because they are fast-moving and difficult to observe long enough to identify and enumerate. Animals were removed after they had been counted, the upper surface of the block was scraped free of foliose algae and sessile invertebrates, and the block replaced in a new position on the reef to create habitat for the subsequent survey period.

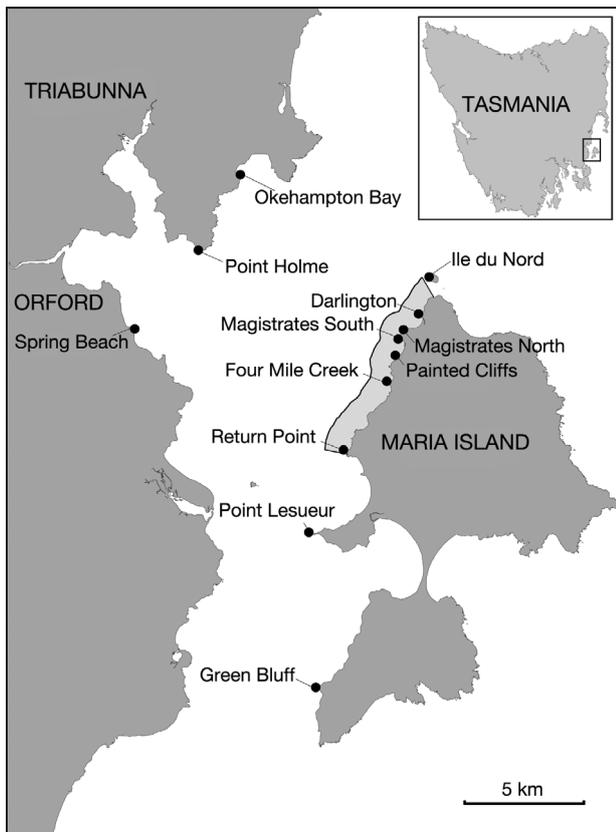


Fig. 1. Locations where blocks were deployed. Lightly shaded region: Maria Island marine reserve. Inset: island state of Tasmania, Australia

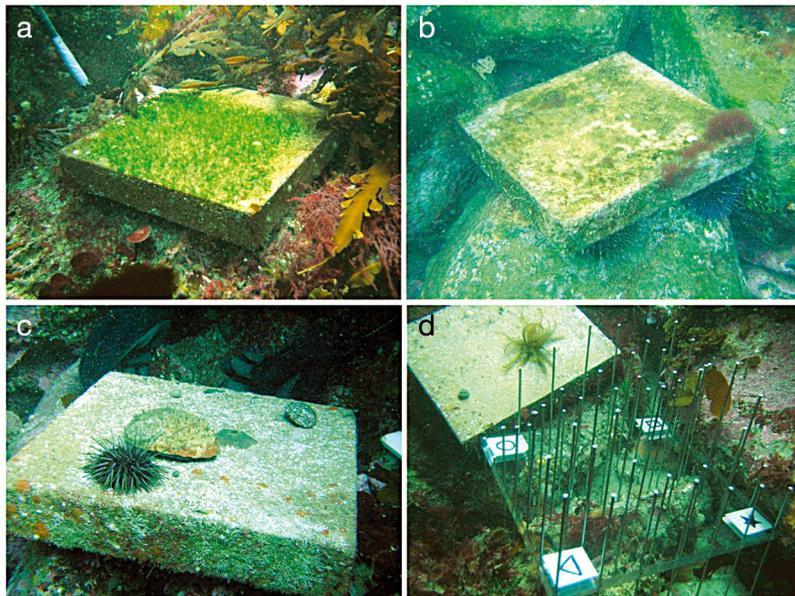


Fig. 2. Blocks *in situ* on the reef surface at (a) Darlington and (b) Point Holme; (c) molluscs and echinoderms attached to the undersurface of a block; (d) profile gauge deployed at block 2, Darlington north (see Fig. 3 for a wireframe representation of this profile)

The shape and volume of the sub-block refuge was quantified for all blocks in the July survey using a profile gauge consisting of a clear acrylic plate ($12 \times 320 \times 320$ mm) with 49 sliding stainless steel pins, each 20 cm length, arranged in a 7×7 grid (50 mm between adjacent pins). This gauge is a 2-dimensional extension of the linear profiling gauge introduced by McCormick (1994). The gauge was deployed in the removed block's position on the reef after animals had been identified and counted (Fig. 2d). The profile gauge was photographed using a housed Olympus 3.2 megapixel compact camera at ~ 12 camera positions around the gauge at an angle of elevation of $\sim 45^\circ$ from horizontal. Photogrammetry was used to identify the position of each pin-head on the z axis where x and y are horizontal axes aligned with 2 sides of the profile gauge plate (Photomodeler Pro 4.0). The x , y and z positions of each of the pin-heads (hereafter points) were exported from the software along with precision, tightness and residual diagnostics. Positional accuracy on the z axis was calculated as < 0.5 cm.

Reef profile calculations

The exported coordinates of the points were used to calculate the surface area of the sub-block profile (Fig. 3), the volume of the refuge space beneath the block, and the vertical cross-sectional area of the space between the perimeter of the block and the reef surface below, hereafter referred to as perimeter access area. The surface area of the profile represents the topographic complexity or the level of 'folding' or convolutions of the reef surface beneath the block (which influences both the volume and the perimeter access area). The volume of space between the block and the reef reflects the potential refuge space available for animals to colonise and the perimeter access area reflects the space around the edge of the block through which predators can access the sub-block refuge. A fourth reef profile metric was calculated as the volume of the sub-block space divided by the total perimeter access area to represent accessibility of the sub-block space relative to the refuge space available.

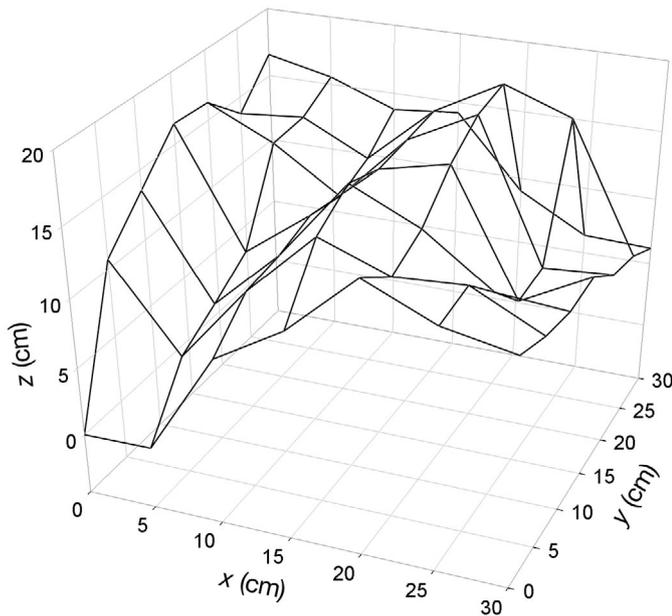


Fig. 3. Wireframe representation of profile data for block 2, Darlington north

Surface area

The surface area of the sub-block profile was calculated using a regular triangular network (Li et al. 2005) by dividing the profile into 36 cells, each delineated by 4 corner points (each cell is 5×5 cm on the horizontal plane; Fig. 3). A fifth pseudo-point was created in the horizontal centre of the cell with a z value (height) of the average of the 4 corner points. Four triangles are then created within each cell by the line joining 2 adjacent corner points and the 2 lines linking each of these to the fifth pseudo-point. The area of each of the 4 triangles was calculated using Herron's formula and then summed to give the surface area of the cell. The surface areas of the 36 cells were summed to give the surface area of the sub-block whole profile. The surface area of a perfectly flat profile ($30 \times 30 = 900 \text{ cm}^2$) was subtracted from the surface area value for each profile to allow meaningful interpretation of intercept in regression analyses.

The calculations using the 4 triangle cell profile were also compared against those based on 2 triangles within each cell, where the longest side of the 2 component triangles is specified as being formed by either the longer or shorter of the 2 cell diagonals. The surface area resulting from these different profile calculations were very highly correlated with each other (surface area calculation on 2 triangles using the longer diagonal versus shorter diagonal;

Pearson's correlation coefficient, $r = 0.999$), and the 4 triangle technique described above ($r = 0.998$), and so were not considered further. The 4 triangle surface was selected over the other 2 as it created a more smooth representation of the surface.

Sub-block volume

In raw form, the x , y , z positions of the points recreate the shape of the reef surface at a distance above the actual reef surface corresponding to the length of the pins. The z height of each pin was subtracted from the z height of the highest pin in the profile (which was usually very close to 18.5 cm — the height of a fully extended pin above the Perspex plate) to give a positive reflection of the surface profile for the calculation of sub-block volume and perimeter access area. The refuge volume was then calculated by approximating the volume beneath each cell as an upright square prism with a width of 5×5 cm and height consisting of the mean of the 4 corner points. The volume for each cell was summed to give a total for the profile.

Perimeter access area

This metric was calculated by breaking the perimeter profile for each side of the plate into a series of shapes formed by 2 adjacent points and the line formed by the edge of the base plate. The area of the shape beneath a line joining each 2 adjacent points was calculated by breaking it into a rectangle and a triangle. The area of the rectangle was calculated as based on a height of the lower of the 2 points and width of the horizontal distance between the 2 points (5 cm). The area of the triangle is calculated as half the horizontal distance between 2 points multiplied by the absolute value of the difference in vertical height for the 2 points. This is repeated for each of the six 2-point intervals on each side of the block, summed to get the perimeter access area for each perimeter side and summed again to give a total perimeter access area for the 4 sides of the profile.

Statistical analyses

Multivariate response data were square-root transformed and assemblages compared based on Bray-Curtis measures of similarity (Bray & Curtis

1957). Unconstrained ordinations in the form of multidimensional scaling were used to visualise the variability of location-aggregated assemblages across space and time. Only species that occurred under >5% of all blocks were considered for block-level multivariate analysis, as preliminary analyses with all data demonstrated that blocks containing only rare species were exerting a disproportionately strong influence on the results. Differences in the cryptofaunal assemblages beneath blocks for locations inside and external to the marine reserve were tested using permutational multivariate analysis of variance (PERMANOVA) (carried out in the PERMANOVA+ add-on to PRIMER 6; Anderson et al. 2008) based on a Bray-Curtis resemblance matrix. Tests were carried out on the data for each season separately using a 3 factor analysis of variance (fixed), location (random, nested in reserve) and site (random, nested in location). Estimates of the components of variation for each spatial scale of the hierarchical sampling design were also calculated for each season. The effects of the marine reserve on univariate responses, including community summary metrics (species richness, total abundance), the abundance of common species and shell length of cryptic *Haliotis rubra*, were also tested by performing a 2-way ANOVA for the location-averaged data, with Survey (random) and Reserve (fixed) as factors. Species abundances were averaged to location to accommodate the high numbers of zero counts underneath individual blocks. ANOVAs were conducted using PERMANOVA based a Euclidean distance resemblance matrix (Anderson et al. 2008).

Distance based linear modelling (DistLM) was carried out to assess the influence of sub-block reef profile characteristics and spatial variation on the invertebrate assemblage. Models were developed based on corrected Akaike's information criterion (AIC_c), which is a modification of Akaike's information criterion (Akaike 1973) for situations where the number of samples is small relative to the number of predictor variables (Anderson et al. 2008). Blocks within locations were expected to be more similar to one another than those from other locations, and this spatial autocorrelation can cause inflated estimates of explained variation if blocks were considered independent samples (Legendre 1993). DistLMs were, therefore, constructed in 2 ways. The initial approach was to determine the contribution of sub-block profile metrics to explaining variance in the invertebrate assemblage, when added to a model with the prior-fitted factor of location. This

reflects the strength of the reef profile metric for explaining variability of cryptofaunal assemblages within locations. Secondly, the location-scale linkages between reef structure and cryptic assemblages were identified by developing DistLMs between the location-averaged profile data and the resemblance matrix for the summed species abundances for each location. For all tests, reef profile calculations were expected to be inter-correlated since they were calculated on the same profile, so model construction never continued beyond the addition of a single reef structure metric.

Relationships between sub-block profile characteristics and (1) the spatial distribution of community summary metrics, and (2) the presence of common and commercially important species, were analysed using generalised linear mixed-effects models (GLMMs; Bolker et al. 2009). The models were used to analyse the contribution of fixed (reef profile metrics) and random (location) factors while acknowledging the non-normality of integer count data and spatial autocorrelation of blocks within locations. A negative binomial distribution is most appropriate for overdispersed count data and was used in the development of models for total invertebrate abundance and species richness. Binomial distributions were used to model the presence-absence of individual species. GLMMs allow inferences to be made about the fixed effects (profile metrics), which represent the average characteristics of the population represented by these samples, and the variability of this relationship amongst locations (Pinheiro & Bates 2000). More simply, these models summarise the relationship between reef structure and the cryptic invertebrate community for blocks within locations. GLMMs were fitted using the *glmmADMB* package in R (R Development Core Team 2009) using AIC to select the reef profile metric that made the greatest contribution to explaining deviance in each response variable. The assumption of a common slope for each location was also tested by fitting a model with random effects for both the intercept and the slope (Pinheiro & Bates 2000). Parallel with the 2-scale assemblage-level multivariate tests, generalised linear models (GLMs) were developed on the location-averaged data using a similar model-building protocol (but using a Gaussian distribution) to determine the capacity of reef structure to explain variability in species richness and total abundance of cryptic invertebrates between locations. Limited replication at the location scale prevented a similar analysis from being carried out on the presence of individual species.

RESULTS

Biological data

A total of 80 species of cryptic molluscs (60) and echinoderms (20) were recorded for the 3 seasonal deployments. Over the course of the study, 15 blocks were damaged or moved by extreme wave action to a position on the substratum where they were unsuitable to survey, leaving a total of 345 samples. The fauna was numerically dominated by gastropods and crinoids (Table 1), with the majority of individuals of each species recorded in higher numbers on the under-surface of the block compared with the reef beneath the unit (1602 and 586 individuals recorded on block and reef surfaces, respectively). The sea cucumber *Australostichopus mollis* was the only species to show a strong preference for the reef underneath the block over the block base (28 ind. on the blocks and 59 on the reef; $p < 0.01$, Wilcoxon signed rank test with paired samples, $n = 65$). No individuals were recorded beneath 43 blocks (12.5%), while the number (mean \pm SE) of species under a block was 3.28 ± 0.12 and the number of individuals was 6.32 ± 0.35 .

The commercially important blacklip abalone *Haliotis rubra* was the third most common species, occurring under 25.5% of blocks (Table 2). The shell lengths of abalone sampled were 11 to 140 mm, with a mean length (\pm SE) of 51.8 ± 1.9 mm. Abalone, like most other species, preferred the underside of the block over the reef surface beneath the block: a total of 23 individuals were found on the reef and 145 individuals on the block surface across all surveys ($p < 0.001$, Wilcoxon signed rank test with paired samples, $n = 87$). No significant difference was evident in the length of abalone on each surface at 47.0 ± 4.6 and 53.5 ± 2.1 mm on reef and block respectively ($p = 0.073$, Welch 2 sample t -test, $n = 87$).

Table 1. Composition of cryptic invertebrate taxa surveyed at all 12 locations over 3 seasonal surveys inside and outside Maria Island marine reserve

Taxon	No. of species	Total no. of ind.
Echinodermata		
Asteroidea	8	191
Crinoidea	2	580
Echinoidea	2	46
Holothuroidea	1	87
Ophiuroidea	7	73
Mollusca		
Bivalvia	1	4
Gastropoda	51	1108
Polyplacophora	8	99

Table 2. Abundance and spatial distribution of the 6 most abundant cryptic invertebrate species under blocks across all surveys inside and outside Maria Island marine reserve

Species	No. of ind.	Occupied blocks (%)
 <i>Allostichaster polyplax</i>	100	19.1
 <i>Australostichopus mollis</i>	87	9.9
 <i>Cenolia trichoptera</i>	525	65.2
 <i>Clanculus limbatus</i>	119	11.6
 <i>Clanculus plebejus</i>	512	33.3
 <i>Haliotis rubra</i>	168	25.5

Results of the variance components analysis were consistent between seasons. The greatest variation in cryptofaunal assemblage composition occurred between blocks separated by several meters (Table 3). Assemblages among various locations differed significantly from each other in all seasons ($p < 0.01$), while sites within each location were not significantly different ($p = 0.251, 0.051, 0.143$ for summer, autumn and winter surveys respectively). Although there was considerable variation of benthic cryptofaunal assemblages between blocks within a location, assemblages at locations were generally more similar to assemblages at the same location for other seasons than other locations (for the same or other seasons; Fig. 4).

Effect of microhabitat characteristics

DistLM of winter survey data identified that the surface area of the reef beneath the block explained the most variation of invertebrate assemblages within locations ($SS = 9762.6$, pseudo- $F_{13,86} = 4.79$, $p < 0.001$, proportion of variance increased from location-only model by 0.03). Surface area of the reef profile also best explained variation in cryptic inverte-

Table 3. Permutational multivariate analysis of variance (PERMANOVA). Analysis of the spatial variance in crypto-faunal invertebrate assemblages between locations, sites and blocks

Survey	Source	Variance	Proportion
Summer	Location	666.11	21.18
	Site	96.30	3.06
	Block	2382.10	75.75
Autumn	Location	796.55	27.82
	Site	156.11	5.45
	Block	1910.40	66.73
Winter	Location	915.13	29.65
	Site	93.95	3.04
	Block	2077.60	67.31

brate assemblage between locations ($SS = 4046.8$, pseudo- $F_{1,10} = 3.32$, $p < 0.05$, proportion of variance explained = 0.249).

Reef structure metrics showed no influence on the number of species recorded beneath blocks within locations or on location-averaged species richness between locations. Variability in reef structure within locations did, however, influence the presence of 4 of the 7 most common species (Table 4). Most species exhibited a positive relationship with reef structure; however, the small trochid *Clanculus plebejus* showed a significant negative relationship with the surface area of the reef profile. Surface area was the most frequently important reef structure metric

across all responses tested, also describing the greatest variability in total invertebrate abundance within (GLMM; Table 4) and between (GLM; $n = 12$, slope = -0.02 , $SE = 0.009$, $t = -2.85$, $p < 0.05$) locations.

Effect of marine reserve

Despite a significant relationship between reef structure and some components of the cryptic invertebrate assemblage, sub-block reef structure did not differ between protected and external locations (PERMANOVA for surface area, pseudo- $F_{1,87} = 0.007$, $p = 0.936$), indicating that the bias of reef structure could be eliminated when testing the effect of the marine reserve for these animals. Indeed, crypto-faunal assemblages were not significantly different between locations inside and external to the marine reserve at any time (Table 5). Species richness, the combined abundance of all invertebrates and the location-averaged abundance of most common species were also not significantly affected by the marine reserve (Table 6). The only response that exhibited a significant relationship with the reserve was the abundance of *Haliotis rubra*, which was higher at locations external to the reserve ($p < 0.05$; Table 6). The mean abundance of this species at protected locations was 50, 29 and 41 % that of fished locations in summer, autumn and winter surveys (Fig. 5). The mean length of cryptic abalone was similar at locations inside and outside the marine reserve (57.1 mm and 52.3 mm respectively; 2-way ANOVA on location-averaged abalone lengths pseudo- $F_{1,22} = 3.47$, $p = 0.218$).

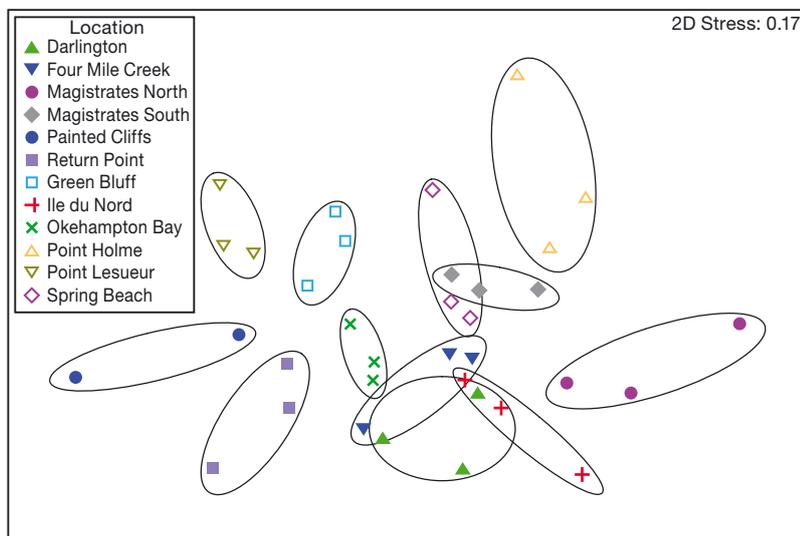


Fig. 4. Multidimensional scaling representing similarity of cryptic invertebrate assemblages between marine reserve (filled symbols) and adjacent fished (open symbols) locations, each surveyed over 3 seasons in 2007

DISCUSSION

The usefulness of concrete blocks as sampling units and the importance for biodiversity of the cryptic component of the benthic community of subtidal rocky reefs are demonstrated by the 80 species of cryptic molluscs and echinoderms surveyed in this study, compared with a total of 46 species of emergent macroinvertebrates accumulated over 10 years of visual censuses at the same sites (Barrett et al. 2009). Concrete blocks are less likely to suffer from the same species bias as other artificial substrata available for sampling subtidal benthic inverte-

Table 4. Generalised linear mixed-effects models (GLMMs) using a negative binomial error distribution to model species richness and total abundance against the sub-block reef structure metrics: surface area, volume, perimeter access area and the ratio between volume and perimeter access area. A binomial (logistic) error distribution was used for the presence-absence of individual species under blocks

Response variable	Optimal model	Slope estimate	SE	z	p
Species richness	Null	–	–	–	–
Total abundance	Surface area	0.03	0.02	1.7	0.089
<i>Allostichaster polyplax</i>	Surface area	–	–	–	0.132
<i>Australostichopus mollis</i>	Volume: perimeter access area	1.93	0.78	2.48	<0.05
<i>Cenolia trichoptera</i>	Surface area	2.46	0.07	3.38	<0.001
<i>Clanculus plebejus</i>	Surface area ^a	–0.18 ^b	0.07	–2.46	<0.05
<i>Clanculus limbatus</i>	Null	–	–	–	–
<i>Haliotis rubra</i>	Null	–	–	–	–
<i>Heliocidaris erythrogramma</i>	Volume	0.07	0.03	2.1	<0.05

^aOptimal model included random effects for both the slope and the intercept
^bMean value around which the slopes for each location randomly varied

Table 5. PERMANOVA output tables for tests of the effect of the marine reserve on benthic cryptofaunal assemblages for each survey. Type III (partial) sums of squares were used with permutation of the residuals carried out under a reduced model

Source	df	SS	MS	Pseudo-F	p
Summer					
Reserve	1	11904	11904	1.95	0.129
Location(Reserve)	9	62686	6965.1	2.58	0.003
Site(Location(Reserve))	11	29830	2711.9	1.14	0.251
Residuals	61	145310	2382.1		
Total	82	253540			
Autumn					
Reserve	1	8284.9	8284.9	0.9559	0.3802
Location(Reserve)	10	93768	9376.8	3.6643	0.0001
Site(Location(Reserve))	12	30803	2567	1.3437	0.0467
Residuals	80	152830	1910.4		
Total	103	290460			
Winter					
Reserve	1	9567.8	9567.8	0.92204	0.4431
Location(Reserve)	10	106000	10600	4.2615	0.0001
Site(Location(Reserve))	12	29878	2489.8	1.1984	0.1398
Residuals	83	172440	2077.6		
Total	106	319810			

brates (Smith & Rule 2002), as the structural complexity of the units is comparable with adjacent natural cryptic microhabitats, the material composition of a block is more similar to adjacent boulders and the unit is resting on a natural reef allowing the easiest and most natural migration route into the sampled space. Indeed, the taxonomic composition of mollusc and echinoderm species sampled in this study was comparable to those surveyed under natural boulders (Chapman 2002a, 2005) and artificially placed blocks (Chapman 2003, 2007) in the intertidal and shallow

subtidal rocky shore. The biota collected by more physically complex artificial substratum such as nylon pan scourers and rope-fibre habitats tend to be numerically dominated by amphipods, bivalves or polychaetes (Edgar 1991, Smith et al. 1996, Smith & Rule 2002, Rule & Smith 2005), presumably a function of the intricate arrangement of microhabitats in these units replicating the structure of complex natural habitats such as foliose macroalgae or kelp holdfasts (Hacker & Steneck 1990). Surprisingly however, similar taxa colonised the fibre-cement artificial crevice habitats of Baronio & Bucher (2008). Although the methods of the present study were focused on sampling molluscs and echinoderms, observations of the units as they were being collected suggested that polychaetes and crustaceans were not frequently encountered in high numbers. Concrete

blocks, therefore, offer a method of surveying cryptic invertebrates on subtidal reefs which target a suite of species complementary to those captured by other artificial substrata sampling techniques.

Effects of microhabitat characteristics

My survey results suggest that concrete blocks are an appropriate tool for sampling broad-scale patterns of cryptic molluscs and echinoderms in subtidal habi-

Table 6. PERMANOVA based on the Euclidean distance resemblance matrix calculated for each univariate response to determine the difference in the cryptofaunal community summary metrics and species abundances for locations inside and external to the Maria Island marine reserve. (* $p < 0.05$; ** $p < 0.01$; no asterisk indicates $p > 0.05$)

Source	df	Species richness		Total abundance		<i>Allostichaster polyplax</i>		<i>Australostichopus mollis</i>	
		MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>
Survey	2	78.9	2.07	4860.8	2.43	31	6.37**	7.3	1.37
Reserve	1	0.1	0	2156	1.08	0.4	0.09	0.8	0.16
Survey × Reserve	2	47.9	1.26	1011.6	0.51	3	0.62	3	0.57
Residual	29	38.1		1999.1		4.9		5.3	
Total	34								

Source	df	<i>Cenolia trichoptera</i>		<i>Clanculus limbatus</i>		<i>Clanculus plebejus</i>		<i>Haliotis rubra</i>	
		MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>	MS	Pseudo- <i>F</i>
Survey	2	65	0.23	71.1	0.88	1100.8	1.55	6.4	0.24
Reserve	1	291.9	1.05	25.8	0.32	1092.5	1.54	187.9	6.90*
Survey × Reserve	2	2.5	0.01	24	0.3	310.5	0.44	6.5	0.24
Residual	29	278.9		80.9		708.7		27.2	
Total	34								

tats, such as for assessment of biogeographic trends (including identification of rare species), or the identification of species richness hotspots and unique assemblages for marine conservation planning. However, significant relationships between characteristics of the reef cavity below deployed blocks and the structure of the invertebrate assemblage (particularly between locations) indicate that the use of blocks for tests of specific environmental effects on cryptic species may be biased for many species if reef

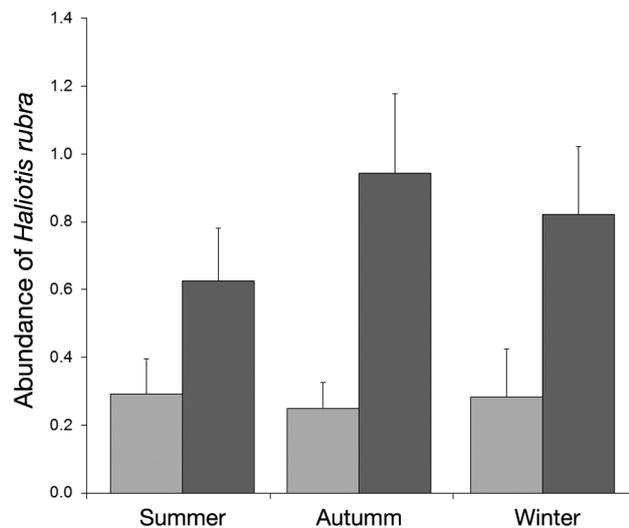


Fig. 5. *Haliotis rubra*. Abundance (mean + SE) of blacklip abalone *H. rubra* under blocks for protected (light grey; $n = 53, 59, 59$) and fished (dark grey; $n = 56, 58, 60$) locations around the Maria Island marine reserve over 3 seasonal surveys in 2007

structure differs systematically between treatments. The relative importance of different structure metrics for each species of the cryptic invertebrate assemblage appears to match body shape and suggests the refuge requirements of the taxon under consideration. A high volume of space beneath a block offers a large 3 dimensional area for animals to colonise. However, a large sub-block space provides little refuge for prey species that rely on their small size to wedge themselves into small cryptic habitats as a defence against predation. The sea urchin *Heliocidaris erythrogramma* exhibited a significant positive association with sub-block volume, probably as it possesses spines as an additional predatory defence and uses cracks and crevices, such as those created between the block and the reef, as a means of enclosing its vulnerable oral surface. The abundance of this species has previously been linked to the density of features of the reef architecture in this region (Alexander et al. 2009). By contrast, the holothurian *Australostichopus mollis* provides an example of a large-bodied cryptic species that has no supplementary defence against predation. This species displayed a significant relationship to the ratio of the volume to perimeter access cross-section, suggesting that it selects or benefits from sub-block refuges that have a large internal volume with limited access for predators from outside.

In my study, sub-block reef surface area had a significant influence on spatial variability of the invertebrate assemblage, the total combined abundance of invertebrates and the presence of the crinoid *Cenolia*

trichoptera. *C. trichoptera* perhaps benefit from high topographic complexity which allows the individuals to conceal their vulnerable oral disc while still offering pathways for the extension of their arms for feeding in the water column. The negative relationship between the trochid *Clanculus plebejus* and surface area reflects the small size of this species (max. width 10 mm; Gowlett-Holmes 2008) and its tendency to occur in high abundances under blocks on near-flat surfaces, which presumably minimise the potential for predator access and attack.

The lack of association between reef structure and the abalone *Haliotis rubra* suggests that concrete blocks can be used to survey and monitor abalone without bias from the shape of the underlying reef. For commercially valuable species such as abalone, an indication of post-settlement density at a site can provide a basis for stock assessment. Corrugated polycarbonate sheets (Nash et al. 1995), venturi suction samplers (McShane & Smith 1988) and boulders contained in crates (Shepherd & Turner 1985), have previously been used to monitor the density of newly settled abalone. However, because abalone suffer mortality rates between 90 and 100% for the first 5 mo after settlement (McShane 1991), such estimates may not reflect the number of adult abalone entering the exploitable stock. Using concrete blocks to sample the abundance of cryptic juveniles that have survived this most vulnerable period could provide a more reliable basis for decisions regarding abalone stock management.

Further development of the use of concrete blocks in the subtidal environment is clearly warranted. Important areas of research include assessment of rates and timing of colonisation of the blocks by species with differing life-history traits, including successional changes in benthic cryptofaunal assemblages over longer periods than studied here. Blocks could also be placed in a more targeted manner to deliberately create particular structural features between the block and the reef. This approach would be particularly useful to isolate and manipulate variability of the different structural metrics investigated here, while holding the other metrics as constant as possible. For example, a position on the reef could be selected to create a large enclosed space with a low perimeter access surface area but high internal volume by placing a block at the junction of 3 or 4 boulders with appropriate spacing and of similar heights. For comparison, blocks could be placed on top of a gently rounded boulder so that the perimeters are open and there is little contained volume within. Such a manipulative approach offers the potential

to characterise associations between slow-moving cryptic species and specific features of the reef architecture within the sub-block space.

Effects of marine reserve

The data presented here provide an example of how deployment of standardized blocks adds an extra dimension to our understanding of distribution patterns of marine communities. Commercially valuable abalone *Haliotis rubra* comprised the only taxon to exhibit a significant marine reserve effect, with this species recorded at significantly lower mean densities at protected locations. These results correspond with a divergence in the numbers of juvenile abalone (30 to 130 mm) between protected and fished locations over time (Barrett et al. 2009). Prior to protection, more mature and juvenile abalone were present at locations to be included within Maria Island reserve boundaries. Over the first 10 yr of protection, numbers declined within the reserve to approximately equal numbers of abalone inside and outside the reserve, with the proportion of juveniles in the population declining dramatically (Barrett et al. 2009). Continued decline in mature abalone numbers since 2002 (Babcock et al. 2010), coupled with data presented here for juveniles, suggest the possibility of a predator-driven Allee effect (Allee et al. 1949) at locations within the reserve. This theory suggests that few adult abalone and the broadcast spawning strategy of this species may result in reduced fertilisation success through a decreased likelihood of the meeting of viable sperm and eggs (Babcock & Keesing 2000).

Allee effects are implicated in the stock collapse of the white abalone *Haliotis sorenseni* and contributed to this species becoming the first marine invertebrate proposed as an endangered species in the United States (Hobday et al. 2000). Populations of *Haliotis laevis* in southern Australia have apparently suffered a similar fate (Shepherd & Partington 1995). The short pelagic larval phase for *Haliotis rubra*, and resulting localised dispersal of propagules (McShane et al. 1988), create the potential for recruitment failure (Tegner et al. 1989) at the protected locations considered in my study. The low abundance of cryptic juvenile abalone at protected locations confirms that recruitment is declining in line with the abundance of mature abalone (Prince et al. 1988) and that, like other gastropod species (Stoner & Ray-Culp 2000), decreased population density is not compensated by increased reproductive output. While the abundance of juvenile abalone was significantly

lower inside the marine reserve, their presence at these sites implies that recruitment was still taking place at the time of my study, indicating that adult densities have not yet passed the critical threshold below which the population cannot sustain itself (Courchamp et al. 1999).

While marine reserves in Tasmania have a dramatic positive effect on the biomass of rock lobster (e.g. Barrett et al. 2009), declining densities of adult abalone combined with reduced recruitment of juvenile abalone at protected locations, indicates that no-take marine reserves may not be the optimal management tool for this species. Species-specific fishery closures on selected reefs may be more suitable to stimulate the growth of populations of species such as abalone that appear to benefit from fishing pressure on their predatory species. This phenomenon does not detract from the net value of marine reserve networks for conservation of species diversity (Alexander & Gladstone 2013), the contribution of unique community types to the seascape (Edgar et al. 2009) and as scientific reference areas for investigation of ecosystem-level effects of fishing.

Acknowledgements. Sincere thanks to J. Seiler, A. Polachek and D. Stephenson for their dedicated assistance in the field and to G. J. Edgar for discussions and constructive criticism of the draft manuscript. The manuscript was also improved by comments from 3 anonymous reviewers. This research was supported by funding from the Australian Research Council, an Australian Postgraduate Award and a CSIRO / University of Tasmania scholarship in Quantitative Marine Science.

LITERATURE CITED

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Caski F (eds) 2nd International symposium on information theory. Akademiai Kiado, Budapest, p 267–281
- Alexander TJ, Gladstone W (2013) Assessing the effectiveness of a long-standing rocky intertidal protected area and its contribution to the regional conservation of species, habitats and assemblages. *Aquat Conserv* 23: 111–123
- Alexander TJ, Barrett N, Haddon M, Edgar G (2009) Relationships between mobile macroinvertebrates and reef structure in a temperate marine reserve. *Mar Ecol Prog Ser* 389:31–44
- Allee WC, Emerson AE, Park O, Park T, Schmidt KP (1949) Principles of animal ecology. WB Saunders Publishing Company, Philadelphia, PA
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Babcock R, Keesing J (2000) Fertilization biology of the abalone *Haliotis laevis*: laboratory and field studies. *Can J Fish Aquat Sci* 56:1668–1678
- Babcock RC, Shears NT, Alcalá AC, Barrett NS, and others (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc Natl Acad Sci USA* 107:18256–18261
- Barnes DKA (2008) A benthic richness hotspot in the Southern Ocean: slope and shelf cryptic benthos of Shag Rocks. *Antarct Sci* 20:263–270
- Baronio Md A, Bucher DJ (2008) Artificial crevice habitats to assess the biodiversity of vagile macro-cryptofauna of subtidal rocky reefs. *Mar Freshw Res* 59:661–670
- Barrett NS, Buxton CD, Edgar GJ (2009) Changes in invertebrate and macroalgal populations within Tasmanian marine reserves in the decade following protection. *J Exp Mar Biol Ecol* 370:104–119
- Barry J, Wickins JF (1992) A model for the number and sizes of crevices that can be seen on the exposed surface of submerged rock reefs. *Environmetrics* 3:55–69
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27: 325–349
- Caillaux LM, Stotz WB (2003) Distribution and abundance of *Rhynchocinetes typus* (Crustacea: Decapoda), in different benthic community structures in northern Chile. *J Mar Biol Assoc UK* 83:143–150
- Chapman MG (2002a) Early colonization of shallow subtidal boulders in 2 habitats. *J Exp Mar Biol Ecol* 275:95–116
- Chapman MG (2002b) Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecol* 27:211–228
- Chapman MG (2003) The use of sandstone blocks to test hypotheses about colonisation 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 (2007) Colonization of novel habitat: tests of generality of patterns in a diverse invertebrate assemblage. *J Exp Mar Biol Ecol* 348:97–110
- Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* 14:405–410
- Drolet D, Himmelman JH, Rochette R (2004) Use of refuges by the ophiuroid *Ophiopholis aculeata*: contrasting effects of substratum complexity on predation risk from two predators. *Mar Ecol Prog Ser* 284:173–183
- Edgar GJ (1991) Distribution patterns of mobile epifauna associated with rope fibre habitats within the Bathurst Harbour estuary, south-western Tasmania. *Estuar Coast Shelf Sci* 33:589–604
- Edgar GJ, Barrett NS (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J Exp Mar Biol Ecol* 242:107–144
- Edgar GJ, Samson CR, Barrett NS (2005) Species extinction in the marine environment: Tasmania as a regional example of overlooked losses in biodiversity. *Conserv Biol* 19:1294–1300
- Edgar GJ, Barrett NS, Stuart-Smith RD (2009) Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. *Ecol Appl* 19:1967–1974

- Gowlett-Holmes K (2008) A field guide to marine invertebrates of South Australia, Notomares, Sandy Bay, Tasmania
- 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
- Griffiths HJ, Linse K, Barnes DKA (2008) Distribution of macrobenthic taxa across the Scotia Arc, Southern Ocean. *Antarct Sci* 20:213–226
- Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285
- Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar Biol* 146:293–299
- Hobday AJ, Tegner MJ, Haaker PL (2000) Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev Fish Biol Fish* 10:493–514
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- Le Hir M, Hily C (2005) Macrofaunal diversity and habitat structure in intertidal boulder fields. *Biodivers Conserv* 14:233–250
- Li Z, Zhu Q, Gold C (2005) Triangular network formation for surface modeling. In: *Digital terrain modeling: principles and methodology*. CRC Press, Boca Raton, FL, p 75–80
- 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
- McCormick MI (1994) Comparison of field methods for measuring surface topography and their association with a tropical reef fish assemblage. *Mar Ecol Prog Ser* 112: 87–96
- McGuinness KA (1984) Species-area relations of communities on intertidal boulders: testing the null hypothesis. *J Biogeogr* 11:439–456
- McGuinness KA (1987a) Disturbance and organisms on boulders I. Patterns in the environment and the community. *Oecologia* 71:409–419
- McGuinness KA (1987b) Disturbance and organisms on boulders II. Causes of patterns in diversity and abundance. *Oecologia* 71:420–430
- McShane PE (1991) Density-dependent mortality of recruits of the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Mar Biol* 110:385–389
- McShane PE, Smith MG (1988) Measuring abundance of juvenile abalone *Haliotis rubra* Leach (Gastropoda: Haliotidae): comparison of a novel method with two other methods. *Aust J Mar Freshw Res* 39:331–336
- McShane PE, Black KP, Smith MG (1988) Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *J Exp Mar Biol Ecol* 124: 175–203
- Metcalf SJ, Dambacher JM, Hobday AJ, Lyle JM (2008) Importance of trophic information, simplification and aggregation error in ecosystem models. *Mar Ecol Prog Ser* 360:25–36
- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Roman F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecol Monogr* 75: 81–102
- Moreira J, Chapman M, Underwood A (2007) Maintenance of chitons on seawalls using crevices on sandstone blocks as habitat in Sydney Harbour, Australia. *J Exp Mar Biol Ecol* 347:134–143
- Nash WJ, Sanderson JC, Bridley J, Dickson S, Hislop B (1995) Post-larval recruitment of blacklip abalone (*Haliotis rubra*) on artificial collectors in southern Tasmania. *Mar Freshw Res* 46:531–538
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-PLUS*. Springer, New York, NY
- Prince JD, Sellers TL, Ford WB, Talbot SR (1988) Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *J Exp Mar Biol Ecol* 122: 91–104
- R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Rule MJ, Smith SDA (2005) Spatial variation in the recruitment of benthic assemblages to artificial substrata. *Mar Ecol Prog Ser* 290:67–78
- Salm RV, Coles SL (2001) Coral bleaching and marine protected areas. *Proceedings of the workshop on mitigating coral bleaching impact through MPA design*. Asia Pacific Coastal Marine Program Report no. 0102, Nature Conservancy, Bishop Museum, Honolulu, HI, p 118
- Shears NT, Babcock R, Salomon AK (2008) Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. *Ecol Appl* 18:1860–1873
- Shepherd SA (1986) Movement of the southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. *Aust J Ecol* 11:295–302
- Shepherd SA, Partington D (1995) Studies on southern Australian abalone (genus *Haliotis*). XVI. Recruitment, habitat and stock relations. *Mar Freshw Res* 46:669–680
- Shepherd SA, Turner JA (1985) Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *J Exp Mar Biol Ecol* 93:285–298
- Smith KA, Otway NM (1997) Spatial and temporal patterns in abundance and the effects of disturbance on under-boulder chitons. *Molluscan Res* 18:43–57
- Smith SDA, Rule MJ (2002) Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? *J Exp Mar Biol Ecol* 277:25–41
- Smith SDA, Simpson RD, Stuart CC (1996) The macrofaunal community of *Ecklonia radiata* holdfasts: description of the faunal assemblage and variation associated with differences in holdfast volume. *Austral Ecol* 21:81–95
- Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239
- Stoner AW, Ray-Culp M (2000) Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar Ecol Prog Ser* 202: 297–302
- Takada Y, Abe O, Shibuno T (2007) Colonization patterns of mobile cryptic animals into interstices of coral rubble. *Mar Ecol Prog Ser* 343:35–44
- Tegner MJ, Breen PA, Lennert CE (1989) Population biology of red abalones, *Haliotis rufescens*, in southern California and management of the red and pink, *H. corrugata*, abalone fisheries. *Fish Bull* 87:313–339