Relationships between mobile macroinvertebrates and reef structure in a temperate marine reserve

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ABSTRACT: Relationships between different metrics of reef structure and the density of macroinvertebrates were examined at 3 nested spatial scales inside and outside a long-established, 'no-take' marine protected area (MPA) at Maria Island, Tasmania, Australia. Generalized linear models were developed that best explained the contributions of rugosity, substratum composition (different-sized boulders, bedrock, sand) and refuge metrics to the spatial variability in invertebrate species richness, total abundance, and the abundances of major taxonomic classes and focal species. To distinguish responses associated with protection from fishing from those relating to natural geographic variation, relationships between reef structure and invertebrate density were also assessed using survey data from before the MPA came into effect. Models combining reef structure and MPA protection explained between 44 to 67 % of spatial variability of total invertebrate abundance across all survey scales examined (1×5, 1×50 and 1×200 m). The number of refuge size categories provided the best predictor of invertebrate species richness at the 5 m scale; however, no reef structure metric investigated was significant at the largest (200 m) spatial scale for species richness. Amongst the explanatory variables examined, MPA protection and density of small refuges generated significant responses for the majority of taxa. One commonly applied metric of reef structure, rugosity, was found to be a relatively poor predictor of invertebrate abundance and richness, generating few significant relationships. Comparisons with pre-MPA data indicated that protection from fishing greatly influenced most major components of the invertebrate community, while reef structure appears to have little interactive influence on these MPA effects at the scales tested here.

KEY WORDS: Rugosity · Spatial refuges · Marine protected area · Sea urchins · Crinoids · Generalized linear model · Species richness · Tasmania

INTRODUCTION

The physical structure of subtidal reefs profoundly affects associated biological assemblages of fish, invertebrates and plants, in part through the provision of refuges from predation (Hixon & Beets 1993, Drolet et al. 2004a), and also through interactions with other environmental factors such as water flow (Shepherd & Partington 1995, Lapointe & Bourget 1999, Pech et al. 2002) and light (Spanier & Almogshtayer 1992, Drolet et al. 2004b). Most research effort examining associations between subtidal reef structure and marine communities has been focused on tropical systems and fish species.

Fish communities in the Mediterranean Sea have been linked to counts of boulders of different size classes (Garcia-Charton & Perez-Ruzafa 1998, Garcia-Charton et al. 2004), to rugosity (La Mesa et al. 2004), and to vertical relief (Garcia-Charton et al. 2004). The diversity of fish communities was found to differ between high and low profile reefs in Western Australia (Harman et al. 2003), while positive correlations were detected between rugosity and the density and diversity of cryptic fish communities in New Zealand (Willis & Anderson 2003).

In the only published community-level study of which we are aware involving relationships between structural complexity and macroinvertebrates on tem-

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perate reefs, boulder size and refuge apertures displayed a weak correlation with fish and no correlation with invertebrate populations on artificial reefs and natural surfaces (Ruitton et al. 2000). Numerically dominant invertebrate species appear to be more closely associated with encrusting algal communities than with reef structure (Ruitton et al. 2000), although the cause of this relationship is uncertain.

The intimate association between benthic macroinvertebrates and reef surfaces would suggest that they should display a close relationship with reef structure. Juveniles of the southern rock lobster *Jasus edwardsii* exhibit a close association with refuges that conform to their body dimensions (Booth & Ayers 2005), as do other panulirid species in Australia (Jernakoff 1990, Dennis et al. 1997) and overseas (Eggleston & Lipcius 1992). Indeed, populations of many crustacean species appear to be constrained by the availability of appropriately sized refuges in the substratum (Wahle & Steneck 1992, Beck 1995, Casariego et al. 2004, Briones-Fourzán et al. 2007). Aggregation characteristics and recruitment of the abalone *Haliotis laevigata* can also be influenced by the shape of the substratum (Shepherd & Partington 1995).

Reef structure has the potential to interact with cascading trophic effects resulting from the return of predatory species to areas of reef protected from fishing. Rock lobsters and large carnivorous fish have been shown to increase in size and abundance in temperate marine protected areas (MPAs) in Tasmania (Edgar & Barrett 1997, 1999, Barrett et al. 2009) and New Zealand (Babcock et al. 1999, Davidson et al. 2002, Shears & Babcock 2002). Structural features such as crevices, holes or overhangs can offer physical refuges to reduce the predatory efficiency of these predators (Drolet et al. 2004a), dampening their impact on prey populations.

Measurements defining the physical structure of subtidal reefs can be divided into 3 broad categories: substratum composition, topographic complexity, and substratum architecture. Most studies of habitat structure in coral reef environments acknowledge the potential influence of the substratum composition on biological communities (Sale & Douglas 1984, McClanahan & Shafir 1990, Friedlander & Parrish 1998, Bergman et al. 2000, Friedlander et al. 2003, Garpe & Ohman 2003). Within the rocky reef environment, different substratum categories can be also defined and quantified (Garcia-Charton & Perez-Ruzafa 2001, La Mesa et al. 2004, Ordines et al. 2005). These generally include consolidated bedrock, a range of boulder size classes, and the percentage cover of sand or gravel.

The most commonly applied measure of topographic complexity or variability of the substratum profile is

rugosity. This is usually quantified as the ratio of the contoured distance along a substratum profile over a known linear horizontal distance (Luckhurst & Luckhurst 1978, Sale & Douglas 1984, McClanahan & Shafir 1990, Friedlander & Parrish 1998, Garcia-Charton & Perez-Ruzafa 1998, Friedlander et al. 2003, La Mesa et al. 2004, Gratwicke & Speight 2005a). The same ratio has also been calculated by measuring the linear distance spanned by a fixed contour length, usually a rope or chain of known length (Dulvy et al. 2002, Harman et al. 2003), or from a profile of regular substratum height measurements relative to a level reference bar (McCormick 1994, Beck 1998).

Substratum architecture refers to the arrangement of angles and planes of the reef creating specific features that have the potential to provide refuges from predation. These include holes (Ault & Johnson 1998, Friedlander & Parrish 1998, Gratwicke & Speight 2005a), crevices (Nemeth 1998) and submarine cliffs or ledges (Bell & Turner 2003). The presence of a refuge at a site can potentially have a large bearing on the community structure if that refuge type enables a large predator (e.g. octopus; Berger & Butler 2001) or habitat-altering species (e.g. the barren-forming *Centrostephanus rodgersii*; Andrew 1993) to colonise and exert their influence in the surrounding area.

Specific features of substratum architecture that create a refuge are difficult to define given the inherently complex nature of the reef surface. The threshold where a refuge qualifies for inclusion in a category is often blurred in nature, a problem overlooked in some studies. Given the range of responses amongst species, no refuge model will be universally applicable to all benthic invertebrates. Nevertheless, measurements can be taken of features of the substratum that are likely to influence a large proportion of the community based on the morphology of the animals and knowledge of the feeding mechanisms of the dominant predators. Enclosing the vulnerable base of the animal (usually feeding and/or attachment mechanism) between 2 or more 'planes' of the substratum would be expected to decrease the success of an attack on most gastropod molluscs and echinoderms. The angle of the meeting of the 2 planes and extent of the divergence will determine the maximum body size of the animal that can use the feature as a refuge. This definition is expanded and applied with representatives of the 2 other categories of measurements described above to quantify the influence of reef structure on mobile macroinvertebrates.

This study aims to characterise relationships between reef structure and fishing on assemblages of mobile macroinvertebrates within a hierarchy of spatial scales. The structure of reefs and associated invertebrates were quantified in the Maria Island marine

protected area (MPA), Tasmania, and nearby reference areas over 2 seasons. This location is particularly appropriate for such a study because of the commercial and recreational importance of 2 of the larger invertebrate species, and the availability of historical ecological monitoring data (Edgar & Barrett 1999). The blacklip abalone *Haliotis rubra* and southern rock lobster *Jasus edwardsii* comprise the most valuable commercial and recreational fishery species in Tasmania, and have shown differing population trends since MPA establishment, with abalone numbers decreasing and rock lobster numbers increasing (Barrett et al. 2009). Historical reef survey data from before the MPA came into effect provide a baseline to assess whether reef structure has influenced the response of benthic invertebrates to prohibitions on fishing.

MATERIALS AND METHODS

Study sites. Field surveys were undertaken in the vicinity of Maria Island, a 20 km long island national park located 6 km off the central east coast of Tasmania, Australia. The geology of the study region is predominantly dolerite with some sandstone. A 'no-take' offshore extension of the Maria Island National Park was declared in September 1991, extending 1 km offshore along 7 km of coast south from the northwestern corner of the island. The resident population on the island consists solely of national park staff, who contributes to the enforcement of the MPA.

Twelve sites were surveyed for mobile invertebrates and reef structure as part of ongoing ecological monitoring of the MPA (Fig. 1; Edgar & Barrett 1997, 1999). Six sites studied within the reserve, Darlington, Magistrates Point North, Magistrates Point South, Painted Cliffs, Four Mile Creek and Return Point, have been closed to fishing since 1991. Six sites external to the reserve were also surveyed: Ile du Nord, Point Lesueur and Green Bluff on Maria Island, and Okehampton Bay, Point Holme and Spring Beach on the adjacent Tasmanian coast. All sites were surveyed in austral spring 2006 (September to October) and autumn 2007 (March).

Survey design. Surveys were carried out along four 50 m long transects set end-to-end parallel to the shore on the 5 m depth contour at each site. Transects consisted of surveyors line with length indicated at 1 m intervals. Lead weights located every 5 m along the line ensured that the line remained in position. Mobile macroinvertebrates and reef structure were surveyed along 4 adjoining 50 m transects in a 1 m swath to one side of the transect line. Within each 50 m transect, a diver swam along the seabed carefully searching for all echinoderms, crustaceans and molluscs larger than
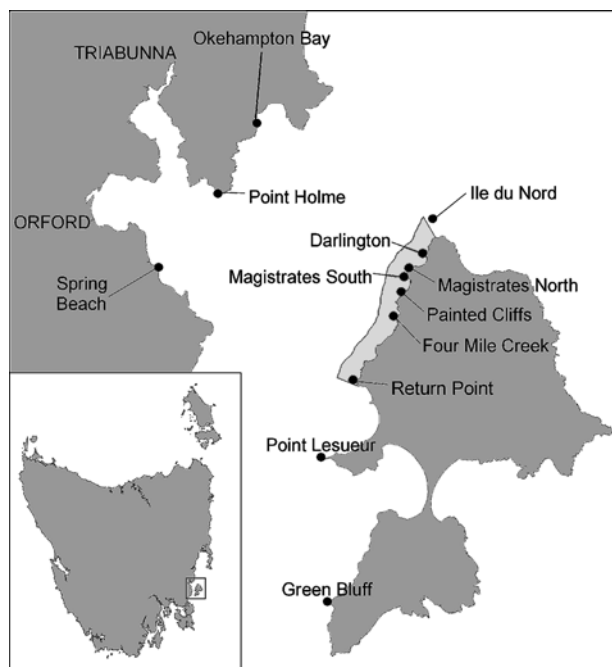

Fig. 1. Map of survey region of Tasmania, Australia. Lightly shaded area indicates the extent of the Maria Island National Park marine extension

1 cm within 1 m of the transect line without moving rocks.

Two 1 × 5 m blocks randomly located within each 50 m transect were also surveyed for invertebrates and reef structure. These different sampling scales allowed us to test the strength of relationships between habitat structure and invertebrates at multiple spatial scales. The two 1 × 5 m blocks also contributed to the average rugosity and refuge density for transect- and site-level tests. These 2 structural variables were time-intensive to measure and impractical to survey along the full transect. Statistical tests were carried out at the block (1 × 5 m), transect (1 × 50 m) and site (1 × 200 m) spatial scales, with block and transect tests consisting of independently surveyed reef structure and invertebrate data. The biological and reef structure data for the four 1 × 50 m transects surveyed at each location were amalgamated for site level tests.

Reef structure assessment. *Substratum composition:* The percent cover of 5 substratum types were visually estimated for all blocks and transects: consolidated bedrock, sand, cobbles (pebbles and rocks with maximum transverse dimension <0.2 m), small boulders (maximum transverse dimension 0.2 to 0.5 m), medium boulders (0.5 to 1.5 m) and large boulders (>1.5 m).

Substratum topographic variability: Variability in the reef surface profile was assessed using a rugosity index. A 5 m length of lead-core nylon rope was con-
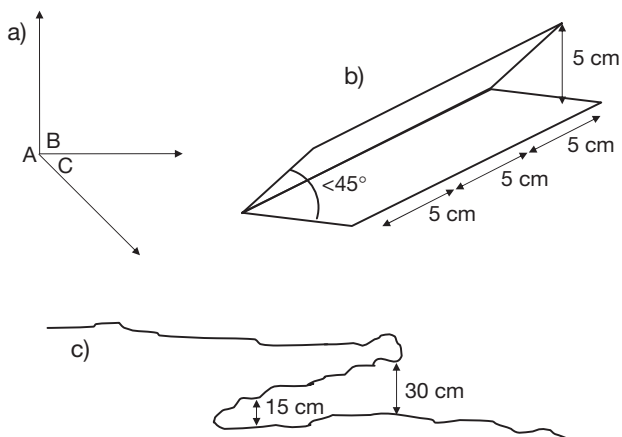
Fig. 2. (a) Representation of a feature of the substratum where 3 planes meet. The feature will be counted as a refuge if ≥1 of angles A, B, and C are <90°. (b) Diagrammatical representation of refuge formed by the meeting of 2 planes at an angle <45°. (c) Cross section of an overhanging ledge or hole that is deeper than the minimum dimension (height in this case) of the aperture. A single refuge can score in multiple size categories—this refuge qualifies in both 6–15 and 16–50 cm categories

toured to the reef surface profile in a line directly underneath the transect from 2 randomly allocated starting points in each 50 m transect block. The linear horizontal span of the contoured rope was measured to the nearest 0.1 m. Rugosity was calculated as: $1 - (L / 5)$, where L = linear distance of 5 m long rope. Because a fixed contour distance was used, this differs from a more commonly used index, where rugosity = contour/ linear distance, as most studies measure rugosity over a fixed linear distance. Taking the inverse of the rugosity formula recovers a linear relationship between the rugosity index and the measured distance, and subtracting it from 1 returns it to the more intuitive relationship of an increase in the structure of the reef equating to an increase in the rugosity index.

Substratum architecture: Substratum architecture was represented by the enumeration of reef features that offered potential refuge to prey species. A working definition of a 'refuge' was developed as (1) the meeting of 3 planes of the substratum with 1 of the planes forming an angle with the other planes of <90° (Fig. 2a), (2) the meeting of 2 planes of the substratum at an angle of 45° or less (Fig. 2b) and (3) the refuge must be deeper than the minimum dimension of its aperture (Fig. 2c).

Refuges were partitioned into 4 size categories by the minimum dimension of the aperture. Size categories were based on an approximate log scale rounded to lengths that could be more readily visually recognised by a diver without measuring implements (1–5, 6–15, 16–50, >50 cm). The biological basis to the selection of these particular size categories was as follows: 1–5 cm: A refuge of this size fully encloses juveniles and the smallest invertebrates and offers protection of the base or 'foot' of most molluscs and echinoderms (T. Alexander pers. obs.); 6–15 cm: Refuge can enclose the body of the majority of invertebrates in the survey region (T. Alexander pers. obs.): 16–50 cm: Features of this scale offer dens for mature rock lobsters (Edmunds 1995)—the dominant invertebrate predator on the reefs; >50 cm: These are large scale features that can have a major influence on light and hydrodynamics (Koehl 2007), and potentially involve caves that offer suitable conditions for the aggregation of fish predators (T. Alexander pers. obs.). The densities of each of these size classes were considered as separate explanatory variables. Refuge 'diversity' was also created as an additional ordinal explanatory variable with levels 0, 1, 2, 3, 4 depending on the number of different refuge size categories represented in the sample. Block level measures were averaged for transect and site.

Additional rules were created to accommodate the real world complexity of the refuge counts. A single refuge can score in multiple size categories if the diverging planes move through multiple size category ranges (Fig. 2c). A refuge can also score multiple counts for a size category if the feature is wider than the upper limits of the size category. For the example given in Fig. 2b, the width is 3 times the height, so this refuge would score 3 times for that size category.

Analyses. Principal component analysis was used to create univariate metrics of the benthic habitat data (i.e. percent cover of large, medium and small boulders, bedrock, sand and cobbles). The scores for the first principal component axis were used as an independent variable in regression analyses (Friedlander & Parrish 1998), thereby reducing the number of independent variables considered for inclusion in the multiple regression models while also overcoming the problem of inter-correlations between percent cover data.

Reef structure–invertebrate relationships at different spatial scales: Multiple regression models were used to determine the contribution of each aspect of the physical environment to spatial variability in the invertebrate community at each spatial scale (Table 1). Multicollinearity is a common property of reef structure measurements, which can cause complications with model fitting, parameter estimation and interpretation. Bivariate scatterplots and correlation matrices were generated to identify strong correlations between explanatory variables and to select the most appropriate representative of intercorrelated groups for inclusion as candidate explanatory variables for model

development. All independent variables were tested for normality with the Shapiro-Wilk test and transformed where appropriate using $\ln(x+1)$ or square root transformations.

Generalised linear models (GLMs) were developed in the statistical package R (R Development Core Team 2007) using stepwise backward elimination of variables. Akaike's information criterion (AIC; Burnham & Anderson 2002) was used to identify the simplest models that explained the maximum amount of variation in the data. An initial Poisson model including all simple explanatory variables (no interaction or higher order terms) was created for each response variable to test the assumption that the mean is approximately equal to the variance as expected under a Poisson distribution of errors. Negative binomial models were employed if significant over-dispersion (variance > mean by a factor of 2) was identified (Ver Hoef & Boveng 2007). At each step, all explanatory variables were considered for elimination from the model if their exclusion contributed to a reduction in the AIC. The explanatory variable whose elimination caused the greatest reduction in AIC was removed from the model and the process continued until the removal of any further variables increased the AIC.

Automated forward stepwise selection of variables was used to confirm that the order of variable elimination did not obscure the search for the most appropriate model. Thus, beginning with the null model, each explanatory variable was considered for inclusion if it contributed to a reduction in AIC. A pseudo-r^2 value was calculated for each final model using 1 – (residual deviance / null deviance) to give an approximate indication of the amount of variance explained by the selected model relative to the null (intercept only) model. Pseudo-r^2 values were somewhat inflated for block and transect level tests due to spatial autocorrelation of samples within a site, and a significance level of $p < 0.01$ was used for single regression tests to attempt to accommodate this. Bivariate scatterplots were used to visually identify non-linear relationships between physical and response variables. Residual plots were used to check for heterogeneous variance and non-linear responses. The interaction between protection status and reef structure measurements were considered for inclusion in the optimal models only at the block level where there was sufficient replication to avoid overfitting.

Optimal multiple regression models were developed at each spatial scale on the combined season data for the community parameters species richness (number of species present in the sample unit), total abundance (combined abundance of all species), for the combined abundance within the major taxonomic groups (Asteroidea, Decapoda, and Gastropoda), and for the numerically dominant sea urchin *Heliocidaris erythrogramma* and feather star *Cenolia trichoptera*. The contribution of reef structure measurements to describe the variability in abundance of the commercially important species, southern rock lobster *Jasus edwardsii* and blacklip abalone *Haliotis rubra*, was also tested at transect and site scales. The sparse distribution of

Table 1. Reef structure measurements tested at the hierarchy of spatial scales. (–) Variable was not considered for inclusion in the models at this scale due to low replication creating a risk of overfitting. MPA: marine protected area; PCA1: principal component analysis

Variable	Block (1 × 5 m)	Transect (1 × 50 m)	Site (1 × 200 m)	Variable description
Rugosity	Directly quantified	Average of 2 block measurements	Average of 8 block measurements	1 – (linear span of 5 m long rope contoured to the reef surface / 5)
PCA1	Based on cover of substratum categories in the block	Based on cover of substratum categories in the transect	Based on combined cover of substratum categories in transects	Scores for the first principal component axis of a principal component analysis on the cover of substratum categories
Dominant habitat[a]	Based on % cover of substratum categories in the block	Based on % cover of substratum categories in the transect	–	Substratum category that contributes the highest % cover in the sample
Small refuges	Directly quantified	Average of 2 block measurements	Average of 8 block measurements	Density of refuges with min. dimension of the aperture 1–5 cm
Refuge diversity[b]	Directly quantified	Average of 2 block measurements	–	No. of refuge size categories represented in the sample
Status	MPA/External	MPA/External	MPA/External	Samples from within MPA or external to the MPA
Season	Autumn/Spring	Autumn/Spring	–	Samples from autumn or spring survey

[a]Substratum categories: consolidated bedrock, sand, cobbles (pebbles and rocks with max. transverse dimension <0.2 m), small boulders (max. transverse dimension 0.2–0.5 m), medium boulders (0.5–1.5 m) and large boulders (>1.5 m). [b]Refuge size categories: min. dimension of aperture 1–5 cm, 6–15 cm, 16–50 cm, >50 cm

these 2 species meant that the block level data contained too many zero counts to warrant testing at this scale.

Single and optimal regression models were also developed for select response variables on 10 random selections of 1 block and transect from each site. This created block and transect data with the same replication as site samples and allowed the use of the pseudo-r^2 to compare the explanatory power of the habitat variables directly across the spatial scales. This also allowed comparisons across the scales free from issues of spatial autocorrelation. The process was limited to responses with low numbers of zero counts at the block scale (species richness, total abundance, *Heliocidaris erythrogramma* and *Cenolia trichoptera*) as random sampling for other responses had the potential to select a dataset with prohibitively high numbers of zeros to allow the use of a consistent error distribution across the scales.

Interactions between protection from fishing and invertebrate–habitat relationships: The long-term influence of the MPA on benthic invertebrates and its interactive relationship with reef structure were tested by comparing the optimal and single regression models, and their respective deviance explained on site level data from 2 historical surveys in 1992 (autumn and spring) with data from the recent surveys in spring 2006 and autumn 2007. The historical surveys were undertaken immediately after the MPA was declared but before effective protection was enforced (Edgar & Barrett 1997). Biological data for each temporal survey were regressed against the average of the reef structure measurements for each site collected during the 2006 and 2007 surveys, with the assumption that reef structure had not changed between historical and recent surveys. These data were averaged to reduce the potential for improved fit of the data for the 2006

Table 2. Importance and composition of the first axis of a principal component analysis (PCA1) on the substratum composition data

	Block	Transect	Site
Importance of component			
Standard deviation	41.4	37.7	33.1
Proportion of variance explained by PCA1	0.588	0.630	0.720
Loadings			
Large boulders	−0.165	−0.177	−0.165
Medium boulders	−0.424	−0.438	−0.448
Small boulders	−0.206	−0.192	−0.194
Cobbles	0	0	0
Sand	0	0	0
Bedrock	0.865	0.859	0.856

and 2007 data, where the reef structure was measured on exactly the same transects as the invertebrate surveys. By comparing the optimal models and individually significant reef structure variables for each of the two 1992 surveys and the 2 recent surveys separately, we could assess the short-term temporal consistency of the relationships and thus interpret the potential long-term effects of the reserve within this context. The significance and details of the changes identified were confirmed by multiple regression analyses of the effects of reef structure on the net change in each response between the average of the 1992 invertebrate surveys and the average of the 2006 and 2007 invertebrate surveys.

RESULTS

A total of forty-three species of large mobile invertebrates were recorded, including 16 shelled gastropods, 9 asteroids, 8 crustaceans, 4 echinoids, 2 crinoids, 2 opisthobranchs, 1 cephalopod and 1 holothurian. Twenty-nine species were recorded in the spring 2006 survey and 33 in autumn 2007. The samples were numerically dominated by the crinoid *Cenolia trichoptera* and the sea urchin *Heliocidaris erythrogramma*. The blacklip abalone *Haliotis rubra* was also recorded in high abundance at many sites.

Principal component analysis on percent cover of substratum categories generated similar outcomes across the surveyed spatial scales (Table 2). The first principal component axis explained from 59 to 72 % of the variance (increasing with spatial scale), with loadings dominated by bedrock (~0.85) and medium boulders (~−0.45) at all scales. Small and large boulders also made negative contributions to the loadings at ~−0.150, while cobbles and sand contributed only trivially to the first principal component axis at all scales. The first principal component thus describes a gradient from generally more complex samples dominated by boulders to those where bedrock is the main substratum. The distribution of substratum types inside and external to the MPA are shown in Fig. 3.

Reef structure–invertebrate relationships at different spatial scales

Invertebrate species richness showed its strongest relationships with reef structure at the finest spatial sampling scale (Tables 3, 4 & 5). Refuge diversity provided the highest pseudo-r^2 (hereafter referred to as r^2) value of 0.304 while the density of small refuges and protection status (samples from protected vs. external sites) also had significant individual influences on spe-
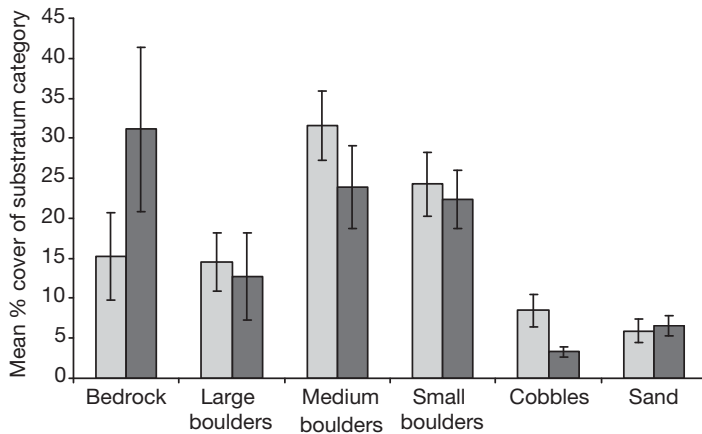
Fig. 3. Substratum types inside (dark grey) and external (light gray) to the Maria Island marine protected area (MPA). Percentages are averaged for 2006 and 2007 surveys

cies richness. A combination of the density of small refuges, refuge diversity, rugosity index and protection status best explained spatial variability of this response at the block level ($r^2 = 0.494$). Invertebrate species richness was significantly lower for transects inside the MPA ($p < 0.01$, $r^2 = 0.143$) with refuge diversity also

only weakly non-significant ($p = 0.057$, $r^2 = 0.065$) at this scale. No explanatory variables were significant at the site level for this data set.

All measured aspects of reef structure had significant individual influence on the spatial variability of the combined abundance of all invertebrate species at all spatial scales (except rugosity at the scale of transect and site; Table 4). The optimal multiple regression models for the block and site levels accounted for >60% of variability in this response. This was slightly weaker at the transect level with 44% variability explained. There was no clear pattern in the strength of the linkage between reef structure and total abundance across spatial scales (Table 5).

The density of small refuges and the sample scores for the first principal component axis (PCA1) were both included in the model that best explained variability of total invertebrate abundance for the 3 spatial scales. PCA1 and small refuges also explained a considerable and similar proportion of variance considered individually at all levels ($r^2 = 0.20$ to 0.45). Protection status explained a statistically significant proportion of the variance at the transect and site scales, with the amount of explained variability

Table 3. Optimal multiple regression models describing the influence of reef structure on mobile invertebrates at different spatial scales around Maria Island. Most models constructed with assumption of negative binomial errors except: [a]Poisson distribution used. A colon indicates a significant interaction between 2 terms

Data	Scale	Optimal model	Pseudo-r^2
Species richness	Block[a]	Refuge diversity – Status + Small refuges – Rugosity	0.494
	Transect[a]	–Status	0.198
	Site[a]	No significant models	–
Total abundance	Block	Small refuges + Refuge diversity – PCA1 + Season	0.674
	Transect	–PCA1 – Status + Small refuges	0.435
	Site	–PCA1 – Status + Small refuges	0.622
Asteroid abundance	Block[a]	–Status – Dominant habitat + Status:Dominant habitat	0.283
	Transect	–Status – Rugosity + Refuge diversity	0.285
	Site	–Status – Rugosity	0.383
Crustacean abundance	Block[a]	–Status – Season + Refuge diversity + PCA1	0.250
	Transect	Refuge diversity – Season + PCA1	0.162
	Site	No significant models	–
Gastropod abundance	Block	–Status – Dominant habitat + Status:Dominant habitat	0.303
	Transect	–Status – Season – Small refuges + Status:Small refuges	0.288
	Site	–Status	0.259
Heliocidaris erythrogramma	Block	Small refuges – Status – Rugosity + Refuge diversity	0.336
	Transect	–Status + Small refuges	0.241
	Site	–Status	0.261
Cenolia trichoptera	Block	Small refuges – PCA1 + Refuge diversity + Status + Rugosity	0.439
	Transect	Dominant habitat + Small refuges – PCA1	0.297
	Site	–PCA1	0.260
Jasus edwardsii	Transect	Status – Season + PCA1 + Rugosity + Status:PCA1	0.481
	Site	Small refuges + PCA1 + Status	0.454
Haliotis rubra	Transect	–Status + Dominant habitat – Small refuges – Season + Status:Small refuges	0.402
	Site	–Status – Rugosity + Status:Rugosity	0.650

increasing in the broader scale samples (r^2 = 0.19 to 0.26). Total abundance of invertebrates was lower for sites surveyed within the reserve boundaries.

Asteroid abundance responded weakly to most measures of reef structure. Only refuge diversity and small refuges were significant at the block level, with the greatest individual r^2 = 0.063 recorded for refuge diversity. Asteroids were significantly more abundant in samples external to the reserve at all spatial survey scales. Reef structure had a weak influence on variability of crustacean abundance, with dominant habitat explaining the most variance of any individual reef structure measurement with r^2 = 0.126 in transects.

Crustaceans were significantly more abundant in blocks external to the MPA ($p < 0.001$, r^2 = 0.083). No measure of reef structure had a significant influence on spatial variability of gastropods, while significantly fewer animals of this class were recorded in samples inside the MPA at all spatial scales.

Reef structure exerted most influence on the abundance of *Cenolia trichoptera* amongst the single species and class abundances studied (Table 4). All single regressions on the combined 2006 and 2007 *C. trichoptera* data for each measure of reef structure at block and transect levels produced significant models. PCA1 was the only reef structure measurement to pro-

Table 4. Single regression models describing the influence of reef structure on mobile invertebrates at different spatial scales around Maria Island. Most models constructed with the assumption of negative binomial errors except: [a]Poisson distribution used. (–) Amount of deviance explained after testing variable was not significantly different from the null model based on chi-squared expectations ($p < 0.05$ for sites; $p < 0.01$ for block and transect to accommodate for spatial autocorrelation between samples within a site). PCA1: principal component analysis

| Data | Pseudo-r^2 for significant single regression tests | | | | | |
Scale	Rugosity	Small refuges	Refuge diversity	PCA1	Dominant habitat	Protection status
Species richness						
Block[a]	–	0.204	0.304	–	–	0.165
Transect[a]	–	–	–	–	–	0.143
Site[a]	–	–		–		–
Total abundance						
Block	0.160	0.449	0.432	0.281	0.278	–
Transect	–	0.214	0.149	0.230	0.179	0.186
Site	–	0.327		0.375		0.260
Asteroid abundance						
Block[a]	–	0.051	0.063	–	–	0.150
Transect	–	–	–	–	–	0.155
Site	–	–		–		0.287
Crustacean abundance						
Block[a]	–	0.071	0.096	–	–	–
Transect	–	–	0.054	–	0.126	–
Site	–	–		–		–
Gastropod abundance						
Block	–	–	–	–	–	0.142
Transect	–	–	–	–	–	0.128
Site	–	–		–		0.259
Heliocidaris erythrogramma						
Block	–	0.151	0.161	0.052	0.159	0.072
Transect	–	0.075	–	–	–	0.183
Site	–	0.135		–		0.261
Cenolia trichoptera						
Block	0.179	0.221	0.224	0.196	0.173	–
Transect	0.122	0.081	0.089	0.184	0.269	–
Site	–	–		0.259		–
Jasus edwardsii						
Transect	–	–	–	0.131	–	0.207
Site	–	–		–		0.330
Haliotis rubra						
Transect	–	–	–	–	0.182	0.244
Site	0.132	–		–		0.439

Table 5. Average pseudo-r^2 for single regressions and optimal models of 10 permutations of 1 randomly sampled block and transect from each site per season. A Poisson error structure was assumed for the species richness models, and a negative binomial error distribution assumed for total abundance and the 2 sets of species abundance models

Response Scale	Rugosity	Small refuges	PCA1	Protection status	Optimal model
Species richness					
Blocks	–	0.267	–	0.248	0.373
Transects	–	–	–	–	0.142
Sites	–	–	–	–	–
Total abundance					
Blocks	–	0.481	0.257	–	0.552
Transects	–	0.259	–	0.225	0.483
Sites	0.163	0.327	0.225	0.260	0.553
Heliocidaris erythrogramma					
Blocks	–	0.216	–	–	0.233
Transects	–	–	–	0.186	0.164
Sites	–	0.135	–	0.261	0.261
Cenolia trichoptera					
Blocks	–	–	–	–	0.304
Transects	–	–	0.153	–	0.213
Sites	0.153	–	0.261	–	0.261

duce a significant relationship with this response at the scale of site (p < 0.01, r^2 = 0.259). *C. trichoptera* abundance was the only response tested that did not display a significant individual response between abundance and protection status at any scale, although this explanatory variable was included in the optimal model at the block level with all other reef structure measurements (excluding dominant habitat). This response showed trends towards stronger linkages with reef structure at the larger spatial scales (Table 5).

The abundance of *Jasus edwardsii*, *Haliotis rubra* and *Heliocidaris erythrogramma* displayed significant relationships to protection status at transect and site levels (Table 4). Spatial variability in the abundance of the southern rock lobster *J. edwardsii* was most consistently explained by a combination of PCA1 and a positive response to protection status. Blacklip abalone *H. rubra* showed little consistent relationships with reef structure and was less abundant in the MPA. The purple urchin *H. erythrogramma* primarily exhibited a negative relationship with the MPA and the density of small refuges.

Interactions between protection from fishing and invertebrate–habitat relationships

Species richness was significantly higher at 'external' sites before the MPA came into effect (Table 6, Fig. 4). This difference was no longer significant in the

2006 or 2007 surveys, a change that was mainly driven by a decrease in species richness at external sites while reserve sites remained steady. Reef structure had no significant influence on species richness at the site level at any time. On the other hand, total invertebrate abundance was significantly related to small refuges in all 4 temporal tests (p < 0.05, r^2 = 0.315 to 0.393 for all 1992 and 2007 surveys). The influence of PCA1 on this response shifted from being non-significant in both 1992 surveys (p = 0.283 and 0.683) to highly significant in 2006 and 2007 (p < 0.001).

Asteroids were more abundant in samples external to the reserve (Fig. 4). This relationship was temporally consistent although protection status also had a significant influence on the net change in asteroid abundance over time (Table 7), with reserve sites remaining steady or dropping slightly while external sites all experienced significant declines in sea star abundance. Few reef structure metrics were significant in the temporal tests for Asteroids or Crustacea; however, a net increase in crustacean abundance at most reserve sites and a slight decrease at most external sites proved to be significant (p < 0.05, r^2 = 0.342). Gastropod abundance was best explained by a combination of PCA1 and protection status in both 1992 surveys (the interaction term indicating a different slope for this relationship inside and external to the reserve). This relationship changed to a combination of small refuges and protection status in 2006 and 2007; however, no significant models explained the net change in gastropods over time (Table 7).

The abundance of *Heliocidaris erythrogramma* decreased substantially at all surveyed sites over the 15 yr interval between the sets of surveys, with the greatest decreases experienced at sites with higher densities of small refuges (optimal model for net temporal change in *H. erythrogramma* abundance was protection status and small refuges, r^2 = 0.369). The change to a negative response to protection status for this species in 2006 and 2007 was particularly influenced by a large decrease in animal numbers between sampling periods at 1 site in the MPA (Four Mile Creek).

Cenolia trichoptera was significantly more numerous external to the MPA in both 1992 surveys. Over the fifteen yr interval this shifted to a negative response to PCA1 in the 2006 and 2007 surveys (Table 6). Protection status strongly explained the net change in the abundance of *Jasus edwardsii* over time (p < 0.01, r^2 = 0.580). Abundance of this species increased at all reserve sites (except an average net decrease of 1 animal at a site on the MPA boundary at Return Point), while all external sites suffered considerable average decreases. Protection status had a significant influence on this species in all temporal samples with its impor-

Table 6. Generalised linear multiple regression models and single regression models describing the influence of reef structure on mobile invertebrates over 15 yr of protection from fishing. Most models constructed using negative binomial errors except when using: [a]Poisson distribution, or [b]quasi-Poisson distribution. (–) Amount of deviance explained after testing variable was not significantly different from the null model based on chi-squared expectations ($p < 0.05$). A colon indicates a significant interaction between 2 terms. PCA1: principal component analysis

Data	Pseudo-r² for significant single regression tests				Optimal model	Pseudo-r²
Survey	Rugosity	Small refuges	PCA1	Protection status		
Species richness						
Aut 1992[a]	–	–	–	0.577	–Status	0.557
Spr 1992[a]	–	–	–	0.566	–Status	0.566
Spr 2006[a]	–	–	–	–	No significant models	–
Aut 2007[a]	–	–	–	–	No significant models	–
Total abundance						
Aut 1992	–	0.315	–	0.267	Small refuges	0.315
Spr 1992	–	0.393	–	0.619	Small refuges + PCA1 – Status	0.811
Spr 2006	–	0.323	0.473	–	–PCA1	0.473
Aut 2007	–	0.347	0.500	0.488	–PCA1 – Status	0.849
Asteroid abundance						
Aut 1992	–	–	–	0.302	–Status	0.302
Spr 1992	–	–	–	0.453	–Status + PCA1	0.605
Spr 2006	–	–	–	0.266	–Status – Small refuges	0.506
Aut 2007	–	–	–	0.333	–Status	0.333
Crustacean abundance						
Aut 1992[b]	–	–	–	0.559	–Status	0.559
Spr 1992	–	–	0.221	–	PCA1 – Status + Status:PCA1	0.785
Spr 2006	–	–	–	–	No significant models	–
Aut 2007	–	–	–	–	No significant models	–
Gastropod abundance						
Aut 1992	–	–	–	–	PCA1 + Status + Status:PCA1	0.496
Spr 1992	–	–	–	–	PCA1 + Status + Status:PCA1	0.400
Spr 2006	–	–	–	0.250	–Small refuges – Status + Status:Small refuges	0.672
Aut 2007	–	–	–	0.299	–Small refuges – Status + Status:Small refuges	0.452
Heliocidaris erythrogramma						
Aut 1992[b]	–	0.247	–	–	Small refuges	0.247
Spr 1992[b]	–	–	–	–	Small refuges + PCA1	0.388
Spr 2006	–	–	–	0.250	–Status	0.250
Aut 2007	–	–	–	0.299	–Status	0.299
Cenolia trichoptera						
Aut 1992	–	–	–	0.214	–Status	0.214
Spr 1992	–	–	–	0.363	–Status	0.363
Spr 2006	–	–	0.344	–	–PCA1	0.344
Aut 2007[b]	–	–	0.596	–	–PCA1	0.596
Jasus edwardsii						
Aut 1992	–	–	–	0.282	Small refuges + Status + Status:Small refuges	0.597
Spr 1992	–	–	–	–	PCA1 + Status + Status:PCA1	0.540
Spr 2006	–	0.335	–	0.336	PCA1 + Status + Status:PCA1	0.823
Aut 2007	–	–	–	0.536	Status + PCA1	0.617
Haliotis rubra						
Aut 1992	–	–	–	–	Rugosity + Status + Status:Rugosity	0.622
Spr 1992	–	–	–	–	No significant models	–
Spr 2006	0.348	–	–	0.399	–Rugosity – Status + Status:Rugosity	0.815
Aut 2007	–	–	–	0.473	–Rugosity – Status + Status:Rugosity	0.732

tance increasing in the recent surveys. *Haliotis rubra* was consistently influenced by an interaction between rugosity and protection status. A significant long-term decrease was evident in the abundance of this species in the MPA relative to external sites ($p < 0.05$, $r^2 = 0.439$).

DISCUSSION

Observational data collected in this study suggest that the mobile invertebrate community around Maria Island is significantly influenced by both reef structure and the protection afforded by the MPA. Most reef
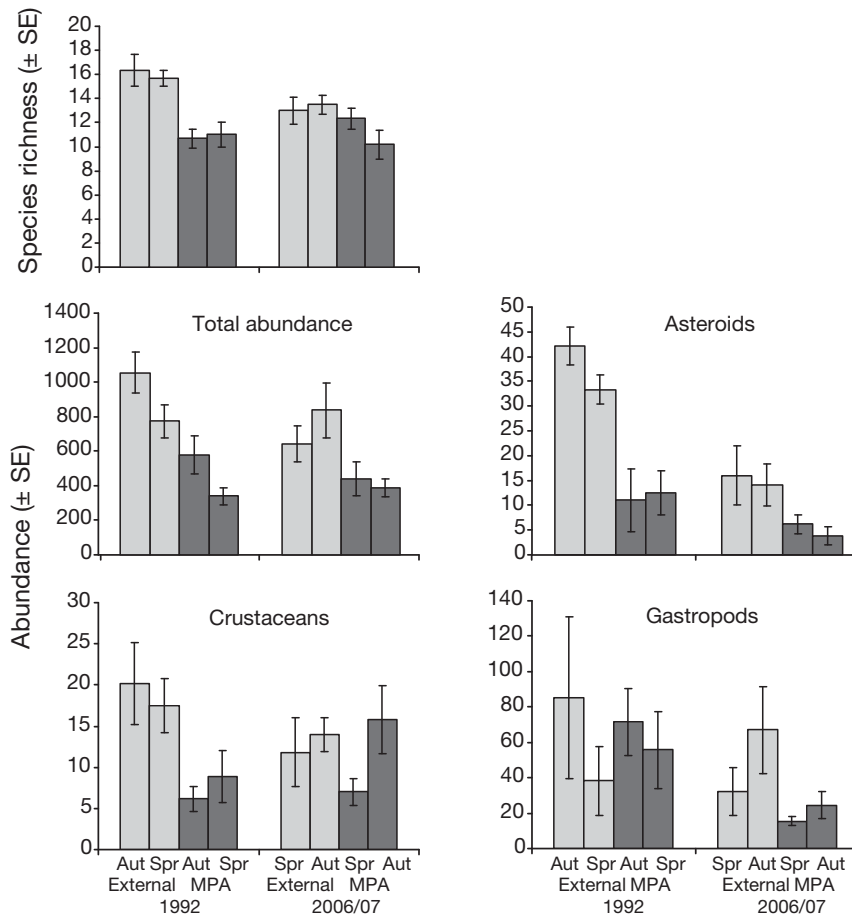
Fig. 4. Mean species richness, total abundance of invertebrates and abundance of 3 of 5 major invertebrate classes (±SE) in sites inside (dark gray) and external to the MPA (light gray) for 2 surveys in 1992 and surveys in 2006 and 2007

dive sites for tourism and conservation awareness.

The density of small refuges and underlying substratum type both explained a large proportion of the spatial variance in invertebrate abundance. High numbers of small refuges in medium boulder dominated habitat (low PCA1 score) supported the largest numbers of invertebrates. The density of small refuges was also the most frequently significant measure of reef structure for other responses. The importance of the presence of refuges echoes the results of other studies where numbers of one or more size classes of holes in coral reefs explained a large proportion of variation associated with fish abundance (Roberts & Ormond 1987) and fish community organisation (Ault & Johnson 1998).

In this study, a refuge was broadly and arbitrarily defined as a type of reef feature that could provide some protection to a resting invertebrate such as a gastropod or sea urchin. Habitats containing a wide range of shapes and sizes of refuges should be expected to offer 'attractive' physical niches to species with a range of body shapes and sizes. This expectation was validated with refuge diversity identified as the measure of reef structure that explained the largest amount of spatial variability of invertebrate species richness at the block level. Similar linkages were not found between the number of refuge size categories and fish communities in a range of shallow tropical marine habitats (Gratwicke & Speight 2005b), perhaps

structure measurements had a positive relationship with total invertebrate abundance across surveyed spatial scales. Patterns in this response variable were largely driven by strong relationships involving 2 conspicuous species, the feather star *Cenolia trichoptera* and sea urchin *Heliocidaris erythrogramma*, which together contributed 88% of total invertebrate abundance in 2006 and 2007. Although total abundance of invertebrates has limited ecological significance, given that small individuals of ephemeral species are allocated the same weighting as large predatory or habitat-engineering species, this metric has relevance when assessing change in MPAs as it provides a community-level index that can represent the public perception of the 'health' of a dive site. A reef is commonly perceived as 'healthy' if a diver observes numerous animals, with implications for the appeal and attractiveness of

Table 7. Multiple linear regression models describing the net temporal change between the average of 2 surveys in 1992 and surveys in 2006 and 2007. Normal distribution of errors assumed and tested in the final model. PCA1: principal component analysis

Response variable	Optimal model	Adjusted r^2
Species richness	Status	0.349
Total abundance	−Small refuges − PCA1	0.543
Asteroid abundance	Status	0.496
Crustacean abundance	Status	0.342
Gastropod abundance	No significant models	–
Heliocidaris erythrogramma	−Status − Small refuges	0.362
Cenolia trichoptera	Status − PCA1	0.354
Jasus edwardsii	Status	0.580
Haliotis rubra	−Status	0.439

because the physical association between marine macroinvertebrates and the substratum is more direct than for fish. A decline in strength of this relationship at the broader sampling scales is most likely attributed to the importance of spatial distribution of refuges to invertebrates. A refuge representing each of the 4 different size classes within 5 m^2 is more ecologically significant than if these refuges are spread over the 50 m extent of a transect.

Rugosity is one of the most commonly measured elements of reef structure in the literature; however, this metric performed poorly in our study, displaying few significant relationships with the response variates tested. One of the few comparable studies relating rugosity to a subtidal invertebrate population was undertaken in tropical waters and reported a negative correlation between sea urchin abundance and rugosity in coral reef lagoons (McClanahan & Shafir 1990). Rugosity has also been recorded as significantly contributing to spatial patterns of diversity, biomass and abundance of fish in some studies (Friedlander et al. 2003, La Mesa et al. 2004), whereas in others weak or no relationship with target fish species have been found (Garcia-Charton & Perez-Ruzafa 1998, Bergman et al. 2000).

The protection offered by the marine reserve had a significant influence on the long-term temporal change in most elements of the invertebrate community tested in this study. Species richness was one of the few responses that was not significantly different between sites inside and external to the MPA in the most recent surveys; however, the 1992 data set indicated that species richness was significantly higher external to the MPA in the 2 surveys before the reserve was effectively policed. Thus, the MPA appears to have been effective at maintaining species richness at approximate 1992 levels while all external sites except Point Lesueur suffered a loss between the average of the 1992 surveys and the recent surveys. These results highlight the importance of pre-MPA data when testing reserve effects (Green 1979, Stewart-Oaten et al. 1986).

Reef structure had relatively little apparent influence on the response of invertebrate populations to MPA protection. Any strong influence should have emerged as a significant interaction between protection status and metrics of habitat structure in regression models of net temporal change (Table 7). Such interactions were, however, present for 6 of the 25 models based on the 2006 and 2007 data (Table 3), notably including models for the 2 commercially important species *Jasus edwardsii* and *Haliotis rubra*. In these cases, interpretation of patterns is difficult without pre-MPA data at block and transect scales. This need for caution is confirmed by some interactions

at the site level that pre-existed protection from fishing (Table 6).

The lack of significant interactions detected through time (Table 7) requires further investigation as it may have resulted from the low number of replicates used for tests, or perhaps been caused by a reduced level of coupling between reef structure and invertebrate community structure at the larger 'site' spatial scale (Garcia-Charton & Perez-Ruzafa 2001). This may also explain why Ruitton et al. (2000) reported a weak relationship between structural complexity and herbivorous invertebrates in their study, which also averaged reef structure measurements to a large scale (2 × 50 m transects).

The protection offered by the MPA appears to have exerted a significant influence on the spatial variability of most responses tested in this study. It is often difficult to conclusively separate MPA effects from biogeographical differences between protected and unprotected sites; consequently, the use of data from before the MPA came into effect greatly strengthens the conclusions presented here. In the 2006 and 2007 surveys, almost all responses at all scales tested in this study displayed a significant difference inside and external to the MPA. The lack of significant influence of protection status in the 1992 surveys for *Haliotis rubra* and *Heliocidaris erythrogramma* supports the premise that more recent significant patterns for these groups are a consequence of 15 yr of protection from fishing.

Total invertebrate abundance was one of the few responses tested where the temporal change was not influenced by the MPA. This may be explained largely by opposing changes in the abundance of *Heliocidaris erythrogramma* and *Cenolia trichoptera* in response to protection. The considerable and universal decrease in numbers of *H. erythrogramma* is most likely driven by a combination of factors. Inside the reserve, the increase in the number and mean size of *Jasus edwardsii* most likely had a negative influence on sea urchin abundance. Juvenile *H. erythrogramma* are predated upon by all size classes of *J. edwardsii*, but only the largest rock lobsters (>120 mm carapace length) are capable of rolling and penetrating the test of large *H. erythrogramma* (Pederson & Johnson 2006) and this is the size class of lobster that has shown the greatest increase in the marine reserve (Barrett et al. 2009). Also, the largest site level increase in abundance of *J. edwardsii* was at Four Mile Creek, which also corresponds to the largest decrease in *H. erythrogramma*. Finally, a small fishery for *H. erythrogramma* (average catch of 100 t yr^{-1} focussed in the south east of the state, DEH 2005), which includes operators based at the nearby fishing port of Triabunna, has potentially contributed to the decrease in the abundance of this species at sites external to the reserve.

Sites supporting high numbers of small refuges experienced the greatest decreases in abundance of *Heliocidaris erythrogramma* over the 15 yr interval. This result was contrary to the expectation that the presence of refuges would provide a buffer against the increased predation pressure inside the marine reserve. Small refuges significantly influenced the abundance of *H. erythrogramma* in both 1992 surveys, but this relationship was no longer present in either 2006 or 2007 surveys. This outcome combined with the significant negative relationship between small refuges and the net temporal change in abundance of *H. erythrogramma* suggests that prior to the reserve, sites with high numbers of small refuges supported large numbers of this species and these are the sites that have suffered the greatest decreases in abundance over time to the point that small refuges no longer have a significant effect in the 2006 and 2007 tests.

Possible causes of the temporal changes in abundance of the crinoid *Cenolia trichoptera* are speculative. The abundance of this species was significantly lower at reserve sites in both surveys before the reserve came into effect. Over the fifteen years between the 2 sets of surveys, the abundance of *C. trichoptera* increased in the reserve, especially at sites dominated by medium boulders (low PCA1), to a stage where the factor 'reserve' is no longer significant. The decrease in abundance and therefore refuge occupation by *Heliocidaris erythrogramma* possibly provided an opportunity for the crinoid to increase in abundance. Sea urchins have been documented as having bulldozing or other clearing behaviours (Andrew & Underwood 1992, Maldonado & Uriz 1998) that could easily be used against the body of a crinoid, and this may have previously inhibited their colonisation of the refuges.

This study provides an exploration of relationships between different elements of reef structure and mobile macroinvertebrate communities in temperate waters. The rationale behind the study was to reduce as many extrinsic sources of environmental variation as possible by sampling at 1 depth strata and over a small geographic range. Additional studies are needed to test the generality of models through analyses based on greater replication over broader scales, allowing for the influences of environmental co-variates such as geology, depth, wave exposure, biological habitat structure (macroalgae) and predator density to be assessed.

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