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Cross-shelf variation in the structure of molluscan assemblages on shallow, rocky reefs in subtropical, eastern Australia

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Abstract Despite the fact that molluscs are one of the most widespread and conspicuous of all marine invertebrates, comparatively little is known about their ecology, especially with respect to biological interactions that drive community processes. We consequently assessed patterns of subtidal mollusc assemblages on subtropical rocky reefs in the Solitary Islands Marine Park (SIMP), eastern Australia. Shelled molluscs (specifically shelled gastropods and bivalves) were targeted to test if: (1) mollusc assemblages change with increasing distance from shore; (2) reef orientation (vertical and horizontal reef faces) influences assemblage structure; (3) sessile benthic communities influence the composition of mollusc assemblages. Multivariate analyses of community patterns indicated strong cross-shelf patterns. However, no significant differences were found for summary community variables (species richness, total abundance). Inshore sites were dominated by large herbivores (especially turbinids) and prey-specific ranellids. Mid-shelf assemblages comprised a mix of taxa that occurred in both inshore and offshore assemblages and were thus transitional between these shelf positions. Offshore assemblages were distinctly different to reefs closer to shore and were characterised primarily by the presence of sedentary (Vermetidae and Chamidae), and tropically-affiliated taxa. Relationships with reef orientations were found to be inconsistent and correlations with sessile benthos were relatively weak. The overall patterns are similar to those found for corals and fish in the region and most likely reflect the increasing influence of the East Australian Current offshore.

Keywords Mollusc ecology · Subtidal · Transition zone · Cross-shelf · Marine Park

Introduction

The study of variation in communities over different spatial scales has been a focal point of marine ecological research for many years (Andrew and Mapstone 1987; McClanahan 1990; Underwood et al. 1991; Bouchet et al. 2002). Measurements of variation at different spatial scales are imperative for the interpretation of ecological studies, as an understanding of this variation facilitates the interpretation and modelling of the ecological processes structuring communities (Underwood and Chapman 1996; Underwood 2000).

Molluscs are well represented in the marine environment, occupying a large range of habitats and ecological niches, and are abundant on shallow subtidal reefs (Gosliner et al. 1996; Zuschin and Piller 1997; Zuschin et al. 2001). Despite this, and the fact that molluscs are a popular taxonomic group, relatively few studies have assessed spatial variation in mollusc assemblages associated

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with subtidal habitats (Gosliner and Draheim 1996; Terlizzi et al. 2003; Wernberg et al. 2008). This is especially the case in Australia where little data exist for areas remote from major cities, or those where there has been focused ecological work (e.g. Great Barrier Reef) (but see Smith et al. 2008).

This trend is undoubtedly linked to the limitations associated with sampling in the subtidal environment (Clarke et al. 2007), where accessibility and time constraints often impede rigorous quantitative sampling. Often, where quantitative studies have been done (McClanahan 1994; Wernberg et al. 2008), they have focused on a single species, a small subset of the assemblage, or on specific taxonomic groups rather than the entire assemblage (Zuschin and Piller 1997; Zuschin et al. 2001). While these studies provide important insight into processes, they do not provide measurements that can be appropriately used at the assemblage level.

The Solitary Islands Marine Park (SIMP) is located on Australia's subtropical eastern coast. It has received scientific attention primarily because it is in a region where tropical Indo-Pacific biota mix with those from southern temperate waters, largely as a result of the influence from the East Australian Current (EAC) (Zann 2000). The influence of the EAC, which is greater at offshore than mid-shelf and nearshore sites (Malcolm et al. 2011), combined with cooler inshore currents, creates a unique mix of tropical, subtropical, temperate, and endemic marine species resulting in high regional diversity (Veron et al. 1974; Harriott et al. 1994; Smith 2000). The interaction between the predominant currents also leads to a clear gradation in sea temperature, with offshore sites experiencing seawater temperatures that are, on average, ~1°C greater than at nearshore sites (Malcolm et al. 2011). Marine assemblages in the region exhibit strong cross-shelf patterns in community structure, as shown for scleractinian corals (Harriott et al. 1994) and fish (Malcolm et al. 2010b). It is likely that mollusc assemblages also show similar patterns—this provides the broad hypothesis for the study reported here.

Even though the SIMP has been a focal point for marine benthic research since the 1970s, there is currently a paucity of quantitative data for mollusc assemblages associated with rocky reefs. This is an important gap, given their prevalence in subtidal habitat and likely role in ecological processes. The objective of this study was therefore to examine variation in mollusc assemblages living on subtidal rocky reefs. Using shelled molluscs, we evaluated whether: (1) the structure of mollusc assemblages changes over a cross-shelf gradient; (2) the orientation of reef structure (vertical and horizontal reef faces) influences assemblage structure; (3) there is a correlation between the structure of mollusc assemblages and sessile benthic communities.

Methods

Study area

This study was conducted within the SIMP on the subtropical mid-north coast, NSW, Australia (Fig. 1). The region supports a full range of subtidal habitats, and rocky reefs cover at least 13% of the sea floor (Marine Parks Authority 2000). There are five main islands within the SIMP, ranging from 2 to 11 km from shore, which have

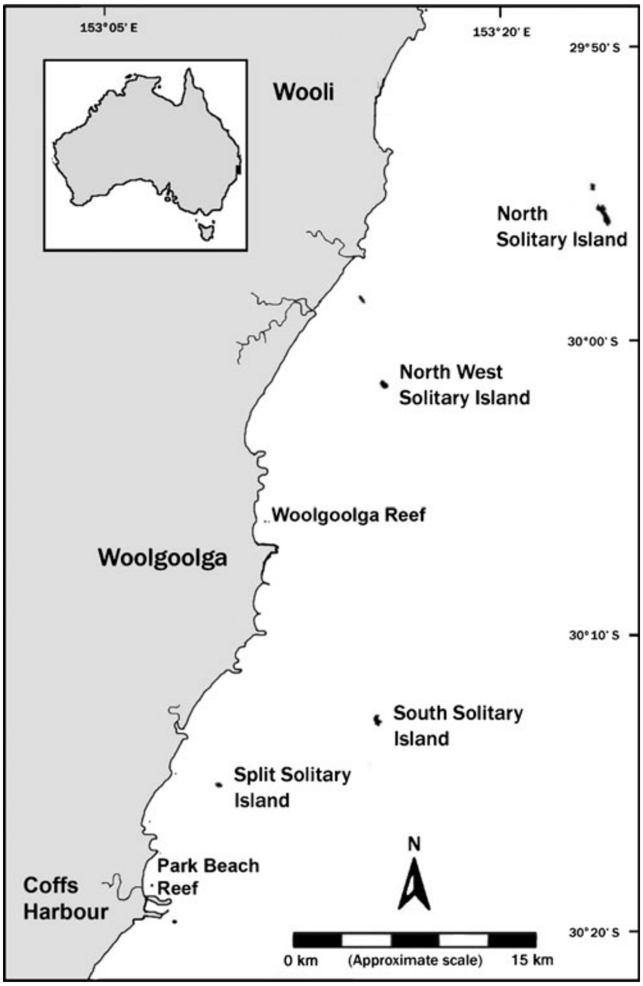

Fig. 1 The Solitary Islands Marine Park (SIMP) showing the six locations sampled in the study: inshore—Woolgoolga Reef and Park Beach Reef; mid-shelf—NW Solitary and Split Solitary Island; offshore—N Solitary and S Solitary

varying degrees of exposure to the prevailing south-easterly swells. This wave climate creates more diverse benthic communities on the sheltered north-westerly sides of islands and coastal headlands (Smith and Simpson 1991; Harriott et al. 1994; Smith 2005). In refining a Habitat Classification System for the SIMP, Malcolm et al. (2010b) demonstrated clear distinctions in reef-associated fish assemblages between nearshore (<1.5 km from shore), mid-shelf (1.5-6 km from shore) and offshore (>6 km from shore) locations. These distance-from-shore strata were consequently recommended as useful boundaries for conservation planning (Malcolm et al. 2010b). Here, we test the hypothesis that similar patterns are evident for molluscan assemblages. Our design therefore targeted replicated locations in each shelf category (referred to as "shelf position" hereafter): inshore—Woolgoolga Reef and Park Beach Reef; mid-shelf—North West Solitary Island (hereafter known as NW Solitary) and Split Solitary Island; offshore—North Solitary Island and South Solitary Island (hereafter known as N Solitary and S Solitary, respectively) (Fig. 1). Sampling sites were selected at a fixed depth of 4-6 m and, thus, reefs at mid-shelf and offshore positions were island-associated. Reefs in this depth-range are characterised by a topography of horizontal to sloping rock shelves and scattered boulder fields. Inshore reefs are commonly dominated by canopy-forming macroalgae, such as the kelp *Ecklonia radiata*, and various erect coralline species. Offshore and mid-shelf reefs are dominated by a mix of hard and soft corals with interspersed areas of turf algae and urchin-grazed barrens (Smith and Simpson 1991; Harriott et al. 1994).

Quantitative surveys

Surveys were carried out between June and August, 2004. Using a nested approach, six locations were selected with two in each of the three shelf positions. Within each location, two sites were established separated by at least 100 m. In each site, horizontal (<45°) and vertical (>45°) aspects were sampled using four randomly placed 5 m^2 (5 × 1 m) transects. This transect size was selected as it has previously been shown to be suitable for large herbivorous molluscs (Vanderklift and Kendrick 2004). The results of a pilot study also showed it adequately sampled the mollusc assemblage (using precision analysis of species richness and abundance data). Each transect was carefully examined making sure to search all habitat features such as cracks and crevices, and behind large motile biota (e.g. the large urchin *Centrostephanus rodgersii*) as they were a consistent refuge for many smaller species (e.g. *Clanculus clangulus* and *Agnewia tritoniformis*). The abundance of all shelled gastropods and bivalves ≥5 mm was recorded. This method was time consuming (individual transects took up to 40 min to search) but necessary to gather comprehensive data. When identification was not possible *in situ*, a voucher specimen was collected for later identification. Some taxa, especially attached bivalves and vermetids, are cryptic or prone to overgrowth by dense epibiota. This makes it difficult to confidently identify them to species without removal from the substratum and/or cleaning. To avoid over-collection (as the work was being done in a marine park), these taxa were recorded only to family level.

Preliminary observations of reefs in the SIMP indicated that benthic community structure potentially influenced the mollusc assemblages present (pers. obs.). In order to examine this relationship, benthic cover was evaluated using photo-quadrats (0.39 m^2) taken haphazardly along each transect. The photo-quadrats were processed using CPCe imaging software (Kohler and Gill 2006). Each photo was assigned ten random points and the benthic taxa present were identified to the highest level of taxonomic resolution possible (species targeted). A total of 100 points in each 5-m^2 transect were assessed and the data summarised as percent cover for each benthic category [list of categories for subtropical reefs adapted from Smith and Edgar (1999)—see Appendix 1].

Statistical methods

Data were analysed using multivariate and univariate permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities and Euclidean distance measures, respectively. This approach was preferred, as the data contained many zeros (Anderson and Millar 2004). These tests use a permutational procedure to calculate a pseudo-F that is a multivariate analogue to the multifactorial, univariate Fisher's F statistic and, in the univariate context, the two are identical when using Euclidean distance as the dissimilarity measure (Anderson et al. 2008). Analyses were performed using a partially-hierarchical, four-factor model: shelf (fixed factor with three levels—inshore, mid-shelf, offshore); aspect (fixed with two levels—vertical and horizontal); location (random and nested in shelf with two levels); and sites (random and nested in locations with two levels). The significance of each source of variation, and the results of pairwise contrasts, were calculated using type III sums of squares and 999 permutations. In cases where an adequate number of unique permutations could not be achieved, Monte Carlo P values, P(mc), were used (Anderson et al. 2008).

The dominance of individual species across the shelf was evaluated by plotting, in rank order, mean abundance of the species that contributed 90% of the total abundance within each shelf position. This approach highlights dominant species and also gives a visual depiction of how the abundance is spread across the assemblage. Univariate analysis was conducted for two summary community measures, species richness (*S*) and total abundance (*N*). Similarities between samples were determined using a Euclidian distance measure, and subsequent analysis was conducted using PERMANOVA. Tests conducted using permutations in this way are sensitive to differences in dispersions (Anderson and Millar 2004). For this reason, homogeneity of the samples was checked using Levene's test prior to analysis and appropriate transformations were made where necessary (Anderson and Millar 2004).

Multivariate data were 4th-root transformed to lessen the influence of abundant species and thus prevent them from dominating the analyses (Field et al. 1982). Analysis followed a standard protocol (Clarke 1993), which first determined the similarity between each pair of samples using the Bray-Curtis similarity measure. Assemblage patterns were then visualised using non-metric multidimensional scaling (nMDS). Due to the large number of sample points ($n=92$), centroids for each site are displayed in the resultant plots, which provides for clearer visualisation of patterns. The variability amongst samples within each shelf position was examined using the Index of Relative Dispersion (IRD) (Warwick and Clarke 1993), which returns an index that has a greater value with increasing variability amongst replicates. The significance of any apparent differences over shelf, aspect, locations, and sites were examined using PERMANOVA. Where appropriate, *a posteriori* pairwise comparisons were conducted to investigate significant terms. No correction was applied to the significance levels of the pairwise tests. This decision was made as corrections normally applied are known to be inexact and conservative (Day and Quinn 1989) and *P* values calculated from the permutation tests provide an exact test of the null hypotheses. In this case, the low number of tests (no more than three for all comparisons) reduces the likelihood of rejecting the null hypotheses simply by chance (Anderson et al. 2008). Where differences were found, identification of the species responsible was assessed using similarity percentage analysis (SIMPER) (Clarke and Gorley 2006). Evaluation of the relationship between the mollusc assemblage and sessile benthic community was conducted using the RELATE procedure. Raw benthic community data were 4th-root transformed and a similarity matrix was created using the Bray-Curtis measure. The RELATE procedure was then used to correlate the matrices for mollusc assemblage and the benthic community using Spearman rank correlation. All analyses were performed in the PRIMER 6.0 package including the PERMANOVA+ add-on (Clarke and Gorley 2006; Anderson et al. 2008).

Results

A total of 1,981 individuals, comprising 91 species from 28 families, was recorded over the study. More species were recorded offshore (68) in comparison with mid-shelf and inshore reefs (38 and 36, respectively). Gastropods accounted for 1,777 individuals and 70 species, and bivalves for 204 individuals and 21 species. Of the 28 families recorded, nine contributed 90% of the total abundance. In the gastropods, the Turbinidae was the most abundant family (605 individuals, four species, 30.8% of total abundance), and the Muricidae were by far the most speciose and the second-most abundant (385 individuals, 15 species, 19.6% of total abundance); together these two families accounted for ~50% of total abundance. The Conidae (seven species) and Columbellidae (six species) were the next most speciose but accounted for <5% of total abundance (82 individuals, combined). The Chamidae was the most abundant family of bivalves (85 individuals, two species, 4.3% of the total abundance) and the Mytilidae (three species) and Pinnidae (three species) were the most speciose families.

Examining the taxa that contributed ~90% of the total abundance (dominant taxa) within each of the shelf assemblages (Fig. 2) indicated that both inshore and mid-shelf assemblages comprised relatively few dominant species (11 and 12, respectively), with less than half of those dominating abundance. In addition, the same species tended to dominate in these shelf positions; only ~25% of species were unique to each shelf position. Dominance was shared by many more species at offshore sites (27 species—Fig. 2), which also supported a much larger proportion of unique species (53% of the total species).

Although there was a trend for offshore sites to support higher mean species richness (Fig. 3), this was associated with high levels of variation, especially between sites at N Solitary. Consequently, there were no significant differences except for the Site[Loc(Sh)] term (Table 1). Pair-wise comparisons indicated that this site difference was only apparent at N Solitary and was due to a much higher richness at Anemone Bay than at Bubble Cave ($t=3.85$, $P<0.01$) (Fig. 3). The mean abundance of assemblages over the shelf did not display any clear trends, even though abundances were slightly higher offshore (Fig. 3). Overall, mean abundance was highly

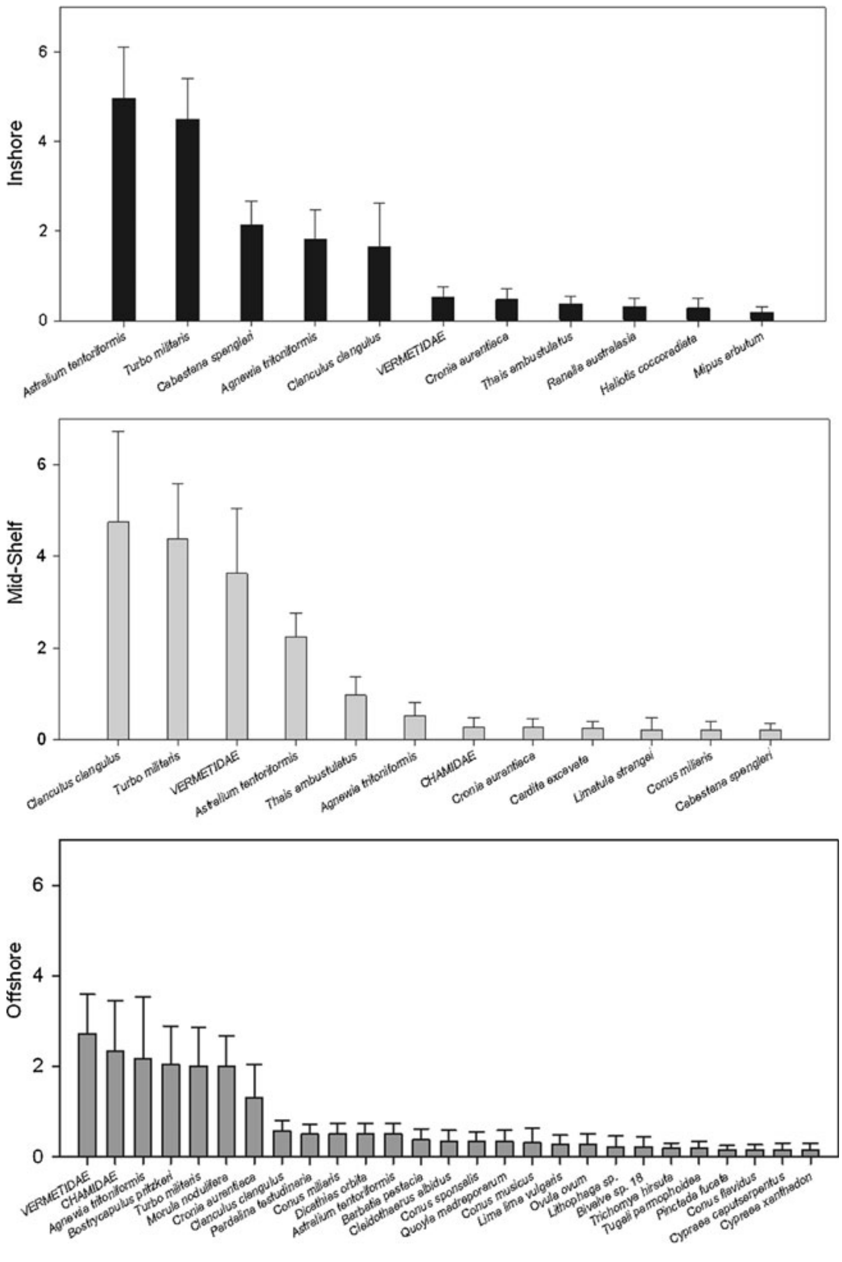

Fig. 2 Ranked mean abundance (5 m²) (+ SE) (dominance) for molluscan taxa contributing 90% of the abundance at different shelf positions

variable, especially between sites within shelf, and there were no significant differences for terms in the analysis (Table 1).

The nMDS analysis showed some obvious patterns of assemblage structure (Fig. 4). Samples from inshore sites group to the left of the plot, those from mid-shelf sites to the middle, with those from offshore sites forming two distinct, island-dependent clusters to the upper and lower right. The 40% similarity contour clearly indicates greater similarity between the inshore and mid-shelf sites than between these and the offshore sites. The analyses of variability amongst samples (IRD) at the scale of shelf indicated increasing variability from inshore to offshore (IRD values: inshore=0.72; mid-shelf=0.92; offshore=1.38). The results of PERMANOVA confirmed the trends in the nMDS indicating significant differences in assemblage structure for shelf, location, and site (Table 1). There was no significant effect for aspect of reef. However, relationships between assemblage patterns and reef aspect varied at the scale of locations potentially confounding the detection of a reef aspect effect (Table 1). The differences amongst shelf positions was primarily a result of the

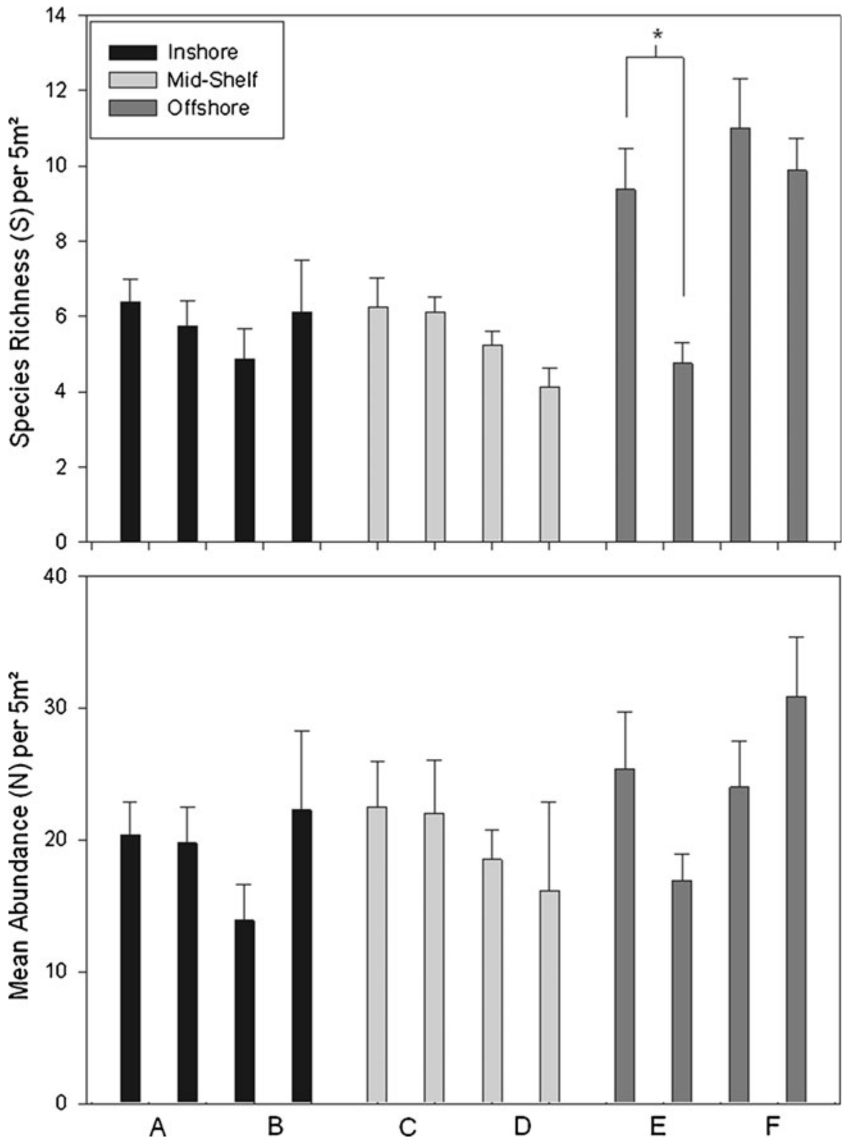

Fig. 3 Mean (+ SE) species richness and abundance of molluscs at each site on inshore, mid-shelf, and offshore reefs (*A* Woolgoolga Reef, *B* Park Beach Reef, *C* NW Solitary, *D* Split Solitary, *E* N Solitary, *F* S Solitary). An *asterisk* indicates a significant difference

Table 1 Summary of multivariate and univariate PERMANOVA tests of *shelf* (fixed factor), *aspect* (fixed factor), *location* (random factor nested within shelf), and *site* (random factor nested within location and shelf) on the structure of mollusc assemblages, species richness, and total abundance. Estimates of components of variation (*cv*) derived from the analysis are reported as percentages of the total. Negative estimates are assumed to be zero (Underwood 1981)

		Assemblage structure			Species richness			Abundance		
Source of variability	*df*	MS	Pseudo-*F*	cv	MS	Pseudo-*F*	cv	MS	Pseudo-*F*	cv
Shelf	2	25,362.00	2.37*	14.21	106.16	2.85 n.s.	19.11	145.51	0.52 n.s.	0.00
Aspect	1	7,045.90	1.65 n.s.	1.79	5.51	0.52 n.s.	0.00	894.26	2.10 n.s.	5.53
Location (Sh)	3	10,688.00	3.32**	14.46	37.22	2.16 n.s.	11.07	279.84	1.39 n.s.	2.76
Sites [Loc(Sh)]	6	3,221.90	1.89**	5.87	19.51	3.46**	13.60	40.82	0.10 n.s.	6.83
ShxAs	2	3,306.30	0.77 n.s.	0.00	17.26	1.83 n.s.	4.90	201.72	1.92 n.s.	0.00
AsxLoc(Sh)	3	4,275.40	2.22**	9.09	10.68	1.90 n.s.	5.59	425.55	2.99 n.s.	20.03
AsxSi[Loc(Sh)]	6	1,928.30	1.13 n.s.	1.71	5.64	1.13 n.s.	1.42	142.51	1.35 n.s.	5.27
Res	72			52.88	5.00		44.32	105.25		59.58

*$P<0.05$, **$P<0.01$, ***$P<0.001$, *n.s.* not significant

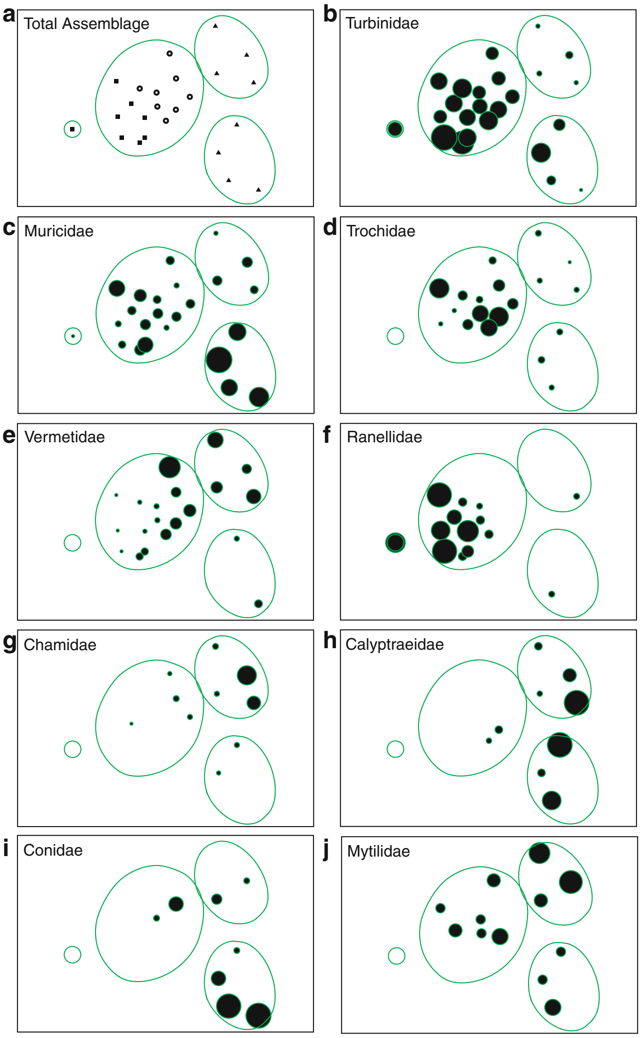

Fig. 4 Non-metric multidimensional scaling ordinations for molluscan assemblages along the cross-shelf gradient. *Unbroken lines* 40% similarity. *Total Assemblage*—centroids for each shelf position: inshore (■), mid-shelf (○), and offshore (▲). Dominant families—bubble size indicates relative mean abundance (i.e. larger bubble = higher abundance)

dissimilarities between inshore and offshore reefs (t=1.84, P<0.05), and mid-shelf reefs did not differ significantly from either inshore or offshore reefs. This indicates a mid-shelf community structure comprising taxa from both inshore and offshore positions.

SIMPER analysis revealed that ten species from seven families accounted for the majority of the dissimilarity between inshore and offshore positions (Table 2). Inshore reefs had higher abundances of Turbinidae, Ranellidae, and Trochidae (Fig. 4), whereas offshore reefs had higher abundances of Vermetidae, Chamidae, Muricidae and Calyptraeidae (Fig. 4). Differences in locations were only detected between reefs at mid-shelf and offshore positions (t=1.94, t=2.42, P<0.01, respectively), and inshore locations showed no significant difference from each other. Eleven species from eight families contributed the majority of the difference between offshore locations (Table 3) with S Solitary having higher abundances of gastropods, especially muricids (Fig. 4). In contrast, N Solitary had much higher abundances of the sessile families Chamidae and Vermetidae (Fig. 4). On mid-shelf reefs, only six species were responsible for the majority of assemblage difference, with NW Solitary having higher abundances of Vermetidae and Chamidae and also the turbinid *Astralium tentoriformis* (Fig. 4). Split Solitary supported a higher abundance of another turbinid species, *T. militaris*, as well as a common muricid, *Thais ambustulatus* (Table 3).

Site differences were not consistent over the shelf and were mostly evident for one inshore (Woolgoolga Reef; t=1.91, P<0.05) and one offshore (N Solitary; t=1.74 P<0.01) location. At N Solitary, nine species contributed the majority of differences, most of which were more abundant at Anemone Bay than Bubble Cave. At Woolgoolga Reef, six species contributed the most to differences between sites, with higher abundances of these species shared between sites.

Correlations between the similarity matrices for benthic communities and mollusc assemblages indicated a significant relationship, although the coefficient was low (ρ=0.25, P<0.01). This indicates that, while there is a significant relationship between benthic communities and mollusc assemblages, other, unmeasured factors are largely responsible for patterns across the scales of this study.

Discussion

This study revealed that mollusc assemblages on shallow subtidal reefs differ depending on their position on the shelf. This observation was predicted at the outset of the study and supports observations from studies of coral and fish assemblages (Harriott et al. 1994; Malcolm et al. 2010b). While patterns for molluscs are slightly less distinct than for fish, the general change in assemblage structure across the shelf (Fig. 4) is consistent across the two broad taxa. The same pattern, of strong overlap between mid-shelf locations and both nearshore and offshore locations, suggesting an ecotone or gradient, is also evident for both taxa (Malcolm et al. 2010b). The primary factor that has previously been used to putatively explain the presence of cross-shelf patterns within this region is the variable influence of the EAC at different shelf positions (Harriott et al. 1994; Malcolm et al. 2010b). In this scenario, offshore locations are more frequently bathed in clear, warm, tropically-derived

Table 2 Results of SIMPER breakdowns for shelf groups (inshore, offshore): mean abundance of the ten highest ranked discriminatory species are shown. Values in *italics* indicate the shelf with the highest mean abundance

	Avg. Diss. 83.56			
	Family	Inshore	Offshore	Contribution (%)
Astralium tentoriformis	Turbinidae	*4.97*	0.50	7.63
Turbo militaris	Turbinidae	*4.50*	2.00	6.90
Vermetidae	Vermetidae	0.53	*2.72*	6.13
Cabestana spengleri	Ranellidae	*2.13*	0.03	5.90
Morula nodulifera	Muricidae	0.00	*2.00*	5.32
Agnewia tritoniformis	Muricidae	1.81	*2.16*	4.61
Chamidae	Chamidae	0.03	*2.25*	4.25
Cronia aurantiaca	Muricidae	0.47	*1.31*	4.15
Clanculus clangulus	Trochidae	*1.66*	0.56	3.94
Bostrycapulus pritzkeri	Calyptraea	0.00	*2.03*	3.80
			Cumulative %	52.63

waters associated with the EAC and this leads to greater tropical influence offshore (Malcolm et al. 2011). This is evident at the broadest scale by the dominance of macroalgae, especially kelp, at inshore sites and the dominance of corals at mid-shelf and offshore sites (Smith and Simpson 1991; Harriott et al. 1994; Malcolm et al. 2010a, b). The patterns observed for mollusc assemblages in this study provide further support for this model.

Assemblages on inshore reefs were relatively consistent across the scale of sites and locations and were dominated by the highly abundant, herbivorous Turbinidae, particularly *Astralium tentoriformis*, and the ranellid *Cabestana spengleri*. It is not surprising that

Table 3 Results of SIMPER breakdowns for locations: mean abundance of species contributing to 50% of the average dissimilarity between locations are shown. Values in *italics* indicate the location with the highest mean abundance

	Avg. Diss. 83.56				Avg. Diss. 64.91		
	Family	N Solitary	S Solitary	Contribution (%)	NW Solitary	Split Solitary	Contribution (%)
Vermetidae	Vermetidae	*4.81*	0.63	6.43	*5.94*	1.31	12.82
Morula nodulifera	Muricidae	0.50	*3.50*	5.71	-	-	-
Agnewia tritoniformis	Muricidae	0.00	*4.31*	5.23	*0.75*	0.31	5.25
Chamidae	Chamidae	*4.25*	0.25	5.04	-	-	-
Turbo militaris	Turbinidae	0.38	*3.63*	4.98	3.13	*5.63*	8.82
Bostrycapulus pritzkeri	Calyptraea	1.88	*2.19*	4.36	-	-	-
Cronia aurantiaca	Muricidae	0.63	*2.00*	4.24	-	-	-
Conus miliaris	Conidae	0.19	*0.81*	3.56	-	-	-
Pardalina testudinaria	Collumbelidae	0.31	*0.69*	3.53	-	-	-
Dicathais orbita	Muricidae	0.00	*1.00*	3.40	-	-	-
Clanculus clangulus	Trochidae	0.56	0.56	3.12	4.75	4.75	10.41
Astralium tentoriformis	Turbindiae	-	-	-	*2.69*	1.81	8.46
Thais ambustulatus	Muricidae	-	-	-	0.75	*1.19*	6.96
		Cumulative %		49.60	Cumulative %		52.72

turbinids are a dominant mollusc in these assemblages as inshore habitats are primarily macroalgal landscapes (Smith and Simpson 1991), and *C. spengleri* is a predator of subtidal ascidians, which are often the dominant suspension feeders on these reefs (Smith and Edgar 1999). The taxa associated with these inshore sites are characteristic of inshore reefs dominated by kelp forests at the broader scale of the NSW north coast region (Smith et al. 2008).

Mid-shelf assemblages were similar to those on inshore reefs but included taxa that were common on offshore reefs; these assemblages were, therefore, transitional between those found on inshore and offshore reefs. Offshore assemblages were distinctly different to reefs closer to shore and were characterised primarily by the presence of sedentary species that were seldom found further inshore, such as *Chama fibula, C. pacifica, Serpulorbis sipho*, and *Bostrycapulus pritzkeri*. The Muricidae were generally dominant offshore, with some species only recorded from these reefs (e.g. *Morula nodulifera*), although there were some species (e.g. *Agnewia tritoniformis*, *Thais ambustulatus*, *Cronia aurantiaca*) that were present in lower abundances closer to shore.

A possible explanation for the shift in assemblage structure on offshore reefs is the presence of the habitat-forming urchin *Centrostephanus rodgersii*, which is known to have high abundance on offshore reefs and relatively lower abundances inshore (Smith and Edgar 1999; Harrison 2003; Posthuma-Gribic 2007). *C. rodgersii* is known to maintain areas of encrusting coralline algal habitat commonly termed “barrens”, through grazing pressure (Underwood et al. 1991; Andrew 1993). Encrusting coralline algal habitat was found to be more extensive on offshore reefs in this study, which supports previous findings within the SIMP (Harriott et al. 1994). The presence of barrens habitat undoubtedly presents the opportunity for sessile species to settle on these reefs, and the continued grazing from *C. rodgersii* prevents these species from being overgrown from various colonizing microalgae and macroalgae. Furthermore, in this study we were able to observe that the presence of *C. rodgersii* facilitates the occurrence of smaller mollusc species (e.g. *Agnewia tritoniformis*, *Clanculus clangulus*, *Cronia aurantiaca*). *C. rodgersii* takes shelter during the day, often using the same refuge; this home-range behaviour leads to bioerosion of the reef at the home site (e.g. large corals), increasing micro-habitat complexity. This phenomenon, coupled with the physical structure of the urchin itself, creates important refuges for smaller molluscs. It is clear that there is an important interaction between *C. rodgersii* and molluscs that depend on the urchin for shelter; experimental investigation is required to shed more light on this.

Another trend within the data was the increased variability amongst sampling sites and locations from inshore to offshore and the clear distinction between assemblages from the two offshore islands. A possible explanation for this pattern is that offshore reefs are more isolated from other reefs on the shelf and thus assemblages are reliant on localised recruitment or sporadic recruitment from the EAC (Rule and Smith 2007). This study also suggests that mixing of the EAC across the shelf may vary latitudinally, with assemblages on northern mid-shelf reefs showing a greater similarity to those on offshore reefs than to those on mid-shelf reefs further south. Recent analyses of seawater temperature at depths of 10 m, and from satellite imagery, provide some support for this hypothesis (Malcolm et al. 2011).

Given the strong patterns found over the shelf, it is surprising that correlations between molluscs and benthic assemblages were relatively weak. It is generally acknowledged that the biological and physical structure of habitats play a role in structuring subtidal communities (Kohn 1968; McClanahan 1990; Pante et al. 2006), and strong associations with the benthos have been demonstrated for inshore molluscs in this region (Smith et al. 2008; Smith and Harrison, unpublished data). The low correlation coefficient in this case can partly be explained by the scale of the photographic sampling method. As the quadrat framer was small, and deployed on the substratum, it is highly likely that the method underestimated the contribution of kelp to benthic communities on inshore reefs. Most of the kelp plant forms a canopy above the substratum; the area of the holdfast, which anchors the kelp to the substratum and was used to quantify kelp cover, occupies only a fraction of the area of a kelp plant. However, recent work on fish assemblages in the region also suggests that specific relationships with benthic communities may well be masked by the strong influence of other factors that covary with distance from shore (Malcolm et al. 2010b).

The orientation of reef substrata is known to play a strong role in structuring the composition of subtidal sessile benthic communities, although its influence can be variable at different spatial scales (Glasby 2000; Glasby and Connell 2001; Knott et al. 2004; Miller and Etter 2011). This study identified that reef orientation had a significant influence on benthic cover, however, the effect of reef orientation was variable between locations and has less of an effect on the mollusc assemblage.

Indeed reef orientation was found to be important for only one sessile species of mollusc, *Bostrycapulus pritzkeri*, which showed a preference for vertical reef faces. Another consideration is that reef habitat sampled in this study was a continuous landscape sloping from horizontal to vertical orientation, sometimes over small spatial scales (< 10 m). On reefs of this type, motile species would be able to move amongst differently-orientated surfaces as needed. Thus, it is not surprising that orientation was more important to sedentary species.

While the patterns at the assemblage scale were strong, univariate summary community measures showed weaker trends with most of the variation associated with sites within each location; there were no significant effects related to shelf position. These results reflect the fact that univariate analyses of species richness and abundance are often less sensitive than multivariate approaches for assessing assemblage changes across an environmental gradient, mainly as they do not take the identity of the species into consideration (e.g. Gray et al. 1990; Smith and Simpson 1992). In this case, the values that were analysed were means for each site; much stronger patterns emerge if the cumulative number of species is considered. Thus, for the same total reef area, the inshore sites had a cumulative species richness of 36, mid-shelf sites of 38 and offshore reefs of 68 species. This pattern is consistent with those found for fish which show a strong positive correlation between species richness and distance from shore (Malcolm et al. 2010a).

The high diversity of marine assemblages in the SIMP has been noted since the 1970s and this is the first study to consider mollusc assemblage patterns over a cross-shelf gradient. This study has shown that the composition of mollusc assemblages changes across the shelf, and that these differences are likely to reflect the influence of the EAC and temperate inshore currents. The cross-shelf pattern is evident as a temperate/endemic assemblage inshore, progressing through a transition zone on mid-shelf reefs, to a variable sub-tropical/tropical assemblage on offshore reefs. This pattern results in unique assemblages on reefs at different positions across the shelf, and promotes a rich diversity of molluscs at a regional scale. Patterns are modified at different shelf positions, most likely by small-scale processes that covary along the cross-shelf transition. These processes require further investigation to better understand their role in structuring mollusc assemblages.

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Appendix

Table 4 Benthic categories used in correlation analysis

Corals
- Acroporidae branching
- Acroporidae encrusting
- Acroporidae plate
- Dendrophylliidae encrusting
- Dendrophylliidae plate
- Faviidae
- Pocilloporidae
- Poritidae
- Other corals branching
- Other corals encrusting
- Other corals plate

Dead corals
- Dead coral with algae
- Recently dead coral

Soft corals
- Soft coral encrusting
- Soft coral massive

Red algae
- *Amphiroa anceps*
- *Corallina berteri*
- *Phymatolithon masonianum*
- Red algae other

Green algae
- *Caulerpa* spp
- *Chlorodesmis* sp.
- *Codium* sp.
- Green algae other

Turfing algae
- Turf

Other invertebrates
- Ascidian colonial
- Ascidian solitary
- Asteriod
- Barnacle
- Bryozoan
- Crinoid
- Echiniod
- Gorgonian
- Hydroid
- Large anemone
- Other invertebrate
- Small anemone
- Sponge encrusting
- Sponge submassive
- Tube worm
- Zoanthid

Substratum
- Bare rock
- Rubble
- Sand
- Sediment

Brown algae
- Ulvaceae
- Brown algae other
- Dictyotaceae
- *Ecklonia radiata*
- *Sargassum* sp.

Mixed sessile assemblage
- MSA

Table 5 Mean abundance of all species at each location within shelf position

	Inshore		Mid-Shelf		Offshore	
Species	Woogoolga Reef	Park Beach Reef	NW Solitary	Split Solitary	N Solitary	S Solitary
Barbatia pistachia	0.00	0.00	0.19	0.00	0.00	0.75
Cardita excavata	0.00	0.00	0.50	0.00	0.06	0.06
Chamidae	0.06	0.00	0.56	0.00	4.25	0.25
Cleidothaerus albidus	0.00	0.00	0.00	0.06	0.44	0.25
Lima lima vulgaris	0.00	0.00	0.00	0.00	0.00	0.56
Limatula strangei	0.00	0.00	0.44	0.00	0.00	0.00
Lithophaga sp.	0.00	0.00	0.13	0.13	0.44	0.00
Modiolus sp.	0.00	0.00	0.00	0.00	0.06	0.00
Trichomya hirsuta	0.00	0.00	0.00	0.00	0.19	0.19
Hyotisa hyotis	0.06	0.00	0.19	0.00	0.00	0.06
Scaeochlamys lividus	0.06	0.06	0.00	0.00	0.13	0.06
Pinna bicolor	0.00	0.00	0.00	0.00	0.00	0.06
Pinna muricata	0.00	0.00	0.06	0.00	0.06	0.06
Streptopinna saccata	0.06	0.06	0.06	0.00	0.13	0.00
Pinctada fucata	0.00	0.06	0.00	0.00	0.00	0.31
Pinctada margaritifera	0.00	0.00	0.00	0.00	0.00	0.06
Bivalve sp. 1	0.00	0.00	0.00	0.00	0.13	0.06
Bivalve sp. 18	0.00	0.06	0.06	0.00	0.44	0.00
Hiatela australis	0.00	0.00	0.19	0.00	0.00	0.00
Bivalve sp. 2	0.13	0.00	0.06	0.00	0.13	0.00
Bivalve sp. 3	0.31	0.00	0.00	0.00	0.00	0.00
Cominella eburnea	0.00	0.06	0.00	0.00	0.00	0.00
Engina armillata	0.00	0.00	0.00	0.00	0.13	0.00
Engina incarnata	0.00	0.00	0.00	0.00	0.06	0.00
Nodopelagia brazeri	0.06	0.06	0.06	0.00	0.00	0.13
Bostrycapulus pritzkeri	0.00	0.00	0.13	0.06	1.88	2.19
Ataxocerithium serotinum	0.00	0.00	0.00	0.00	0.25	0.00
Columbellidae sp. 1	0.00	0.00	0.00	0.00	0.06	0.00
Columbellidae sp. 2	0.00	0.00	0.00	0.00	0.06	0.00
Euplica varians	0.00	0.00	0.00	0.00	0.06	0.00
Pyrene flava	0.00	0.00	0.00	0.00	0.00	0.06
Pardalina testudinaria	0.06	0.00	0.31	0.00	0.31	0.69
Pyrene turturina	0.00	0.00	0.00	0.00	0.13	0.06
Conus capitaneus	0.00	0.00	0.00	0.00	0.00	0.06
Conus flavidus	0.00	0.00	0.00	0.00	0.00	0.31
Conus lividus	0.00	0.00	0.00	0.00	0.06	0.00
Conus miles	0.00	0.00	0.00	0.00	0.00	0.13
Conus miliaris	0.00	0.00	0.38	0.06	0.19	0.81
Conus musicus	0.00	0.00	0.00	0.00	0.00	0.63
Conus sponsalis	0.00	0.00	0.00	0.00	0.00	0.69
Cypraea caputserpentis	0.25	0.00	0.00	0.06	0.00	0.31

Table 5 (continued)

	Inshore		Mid-Shelf		Offshore	
Species	Woogoolga Reef	Park Beach Reef	NW Solitary	Split Solitary	N Solitary	S Solitary
Cypraea clandestina	0.00	0.00	0.00	0.00	0.00	0.06
Cypraea vitellus	0.00	0.00	0.00	0.00	0.00	0.06
Cypraea xanthodon	0.00	0.19	0.00	0.00	0.00	0.31
Latirus polygonus	0.00	0.00	0.00	0.00	0.00	0.06
Tugali parmophoidea	0.00	0.00	0.00	0.00	0.06	0.31
Haliotis coccoradiata	0.00	0.56	0.06	0.19	0.06	0.06
Mitra carbonaria	0.00	0.00	0.19	0.00	0.00	0.00
Mitra scutulata	0.00	0.00	0.06	0.00	0.00	0.00
Mitra sp. 1	0.00	0.00	0.00	0.00	0.00	0.06
Agnewia tritoniformis	1.50	2.13	0.75	0.31	0.00	4.31
Chicoreus denudatus	0.00	0.06	0.00	0.00	0.00	0.00
Cronia aurantiaca	0.75	0.19	0.31	0.25	0.63	2.00
Cronia contracta	0.00	0.00	0.00	0.00	0.00	0.06
Cronia margariticola	0.00	0.00	0.00	0.00	0.06	0.00
Lepsiella reticulata	0.06	0.00	0.00	0.00	0.00	0.00
Mipus arbutum	0.31	0.06	0.00	0.00	0.00	0.00
Morula nodulifera	0.00	0.00	0.00	0.06	0.50	3.50
Morula spinosa	0.00	0.00	0.00	0.06	0.00	0.00
Pascula ochrostoma	0.00	0.00	0.00	0.00	0.00	0.31
Quoyula madreporarum	0.31	0.00	0.06	0.25	0.63	0.06
Thais alouina	0.00	0.00	0.00	0.00	0.00	0.19
Thais ambustulatus	0.38	0.38	0.75	1.19	0.00	0.13
Dicathais orbita	0.13	0.06	0.00	0.25	0.00	1.00
Thais tuberosa	0.00	0.00	0.00	0.00	0.06	0.00
Drupella cornus	0.00	0.00	0.00	0.00	0.06	0.00
Ovula costellata	0.00	0.00	0.00	0.00	0.13	0.00
Ovula ovum	0.00	0.00	0.00	0.00	0.13	0.44
Scutellastra chapmani	0.00	0.25	0.00	0.00	0.00	0.00
Cabestana spengleri	1.38	2.88	0.00	0.44	0.06	0.00
Charonia lampas rubicunda	0.06	0.00	0.00	0.00	0.00	0.00
Cymatium exaratum	0.00	0.06	0.00	0.00	0.00	0.00
Ranella australasia	0.38	0.25	0.00	0.00	0.00	0.06
Siphonaria sp.1	0.00	0.00	0.06	0.00	0.00	0.00
Astele sp. 1	0.00	0.00	0.00	0.00	0.06	0.00
Calliostoma legrandi	0.00	0.00	0.00	0.00	0.00	0.19
Clanculus clangulus	0.13	3.19	4.75	4.75	0.56	0.56
Eurytrochus strangei	0.00	0.06	0.00	0.00	0.06	0.00
Herpetopoma aspersa	0.00	0.31	0.00	0.06	0.00	0.00
Astralium tentoriformis	8.19	1.75	2.69	1.81	0.44	0.56
Turbo militaris	4.31	4.69	3.13	5.63	0.38	3.63
Turbo torquatus	0.31	0.00	0.00	0.00	0.00	0.00
Turbo undulatus	0.00	0.00	0.00	0.31	0.00	0.00
Austrodrillia angasi	0.00	0.06	0.00	0.00	0.00	0.06
Heliacus variegatus	0.00	0.00	0.13	0.00	0.00	0.00
Mitre sp.1	0.00	0.00	0.00	0.00	0.31	0.00
Columbellidae sp. 3	0.00	0.00	0.06	0.00	0.00	0.00
Notogibbula bicarinata	0.00	0.31	0.00	0.00	0.00	0.00

Table 5 (continued)

Species	Inshore		Mid-Shelf		Offshore	
	Woogoolga Reef	Park Beach Reef	NW Solitary	Split Solitary	N Solitary	S Solitary
Notoacmea flammea	0.00	0.00	0.00	0.06	0.00	0.00
Vermetidae	0.81	0.25	5.94	1.31	4.81	0.63
Micromelo undata	0.00	0.00	0.00	0.00	0.06	0.00

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