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# A preliminary investigation of diversity, abundance, and distributional patterns of chitons in intertidal boulder-fields of differing rock type in South Australia

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Running head: Chitons in boulder-fields of differing rock type

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## Abstract

The rock type of hard-substrata marine habitats can affect numerous benthic invertebrates, but little is known of the effects on molluscan assemblages, for example, the chitons often found under intertidal boulders. We compared chiton assemblage composition, abundance, species richness, and patterns of frequency distribution in ten boulder-fields containing either hard metamorphic/igneous boulders or soft limestone boulders, in two geographical areas in South Australia. Similar species richness occurred in both types of boulder-fields, but hard rock boulder-fields had greater overall abundances, because of particularly large abundances of some common species. Differences in abundances of common species also resulted in significantly different assemblages occurring between the boulder-field types. Some species appeared aggregated among boulders, but this pattern was variable between boulders in differing areas and of differing rock type. In one area, a common species had variable aggregation that caused frequency distributions to differ significantly between boulders of different rock types. These results indicate that rock type needs to be considered when investigating ecological patterns and processes involving specialist molluscs such as under-boulder chitons, and to ensure comprehensive marine reserve planning for protecting rare invertebrates in rocky intertidal reefs.


## Introduction

Environmental features within species habitats are often key in setting patterns of distribution in populations. For rocky benthic assemblages, the physical composition and structure of the rock substratum is often important. Varying surface heterogeneity can influence the choices for settlement sites of invertebrate larvae, and the subsequent recruitment of juveniles and adults (Le Tourneux and Bourget 1988; Kohler *et al.* 1999; Berntsson *et al.* 2000). Post-recruitment processes can also be affected by the structure of the substratum, such as movement (Chapman and Underwood 1994; Underwood 2004), mortality (Herbert and Hawkins 2006), and growth (Giesel 1969; Gosselin and Bourget 1989). The rock type of the substratum is one factor that can affect numerous benthic taxa, including barnacles (e.g. Herbert and Hawkins 2006), tube worms (e.g. James and Underwood 1994), urchins (e.g. Bavestrello *et al.* 2000), and algae (e.g., McGuinness and Underwood 1986). An early descriptive account of the presence/absence of intertidal mollusc species over a large area in

the tropical Pacific suggested that many molluscs have associations with specific rock types (Vermeij 1971). Since then, only a small number of studies have investigated effects of rock type on molluscs (Table 1) with some studies finding rock type has an effect and others not. In particular, Vermeij (1971) suggested that molluscs with large areas of soft tissue in contact with the substratum (e.g., limpets and chitons) can be expected to have strong associations with specific rock types because variable aspects of the rock substratum may affect their capacities for movement (Erlandsson *et al.* 1999), orientation (Garrity and Levings 1983; Fraser *et al.* 2010), and attachment (e.g., Grenon and Walker 1981). Although many benthic molluscs occur in regions with diverse natural rock types, this factor is seldom investigated as a determinant of patterns in their distribution.

<TABLE 1 ABOUT HERE>

A particularly wide range of mollusc species occur in the habitats on intertidal boulders. When moveable rocks are present in the intertidal zone, a range of mobile and sessile species are often found on the upper- and under-sides of the rocks (McGuinness and Underwood 1986; Todd and Turner 1986; Chapman 2007) and on the underlying substratum (Todd and Turner 1986). Sometimes intertidal boulders occur on their own (e.g. within small rock pools), but most often they are clustered together on patches of shore called ‘boulder-fields’, that can be a few or many square metres in area.

Some species in boulder-fields are also commonly found in other intertidal habitats (e.g. snails and limpets that occur on uppersides of boulders, and also on stable rock platforms; McGuinness and Underwood 1986), while others appear to be boulder-field specialists, and are rarely found elsewhere (Kangas and Shepherd 1984; Chapman 2011). This is particularly the case for a range of chitons (Polyplacophora: Mollusca) that are found almost exclusively underneath boulders, where they are at less risk from predation (Shepherd and Clarkson 2001). Some species of under-boulder chitons are rare and considered threatened. For example, the documented extent of distribution for one species, *Bassethullia* (Pilsbury, 1928) *glypta* (Sykes, 1896), is confined to a small area at the entrances of two bays in south eastern Australia (O'Hara 2002). The rarity and endemicity of many species in boulder-fields, and the susceptibility of the habitat to disturbance (e.g., Addessi 1994; Le Hir and Hily 2002), has led to an increasing number of authors acknowledging that the habitat requires priority in coastal conservation programmes (Thompson *et al.* 2002; Benkendorff and Davis 2004; Banks and

Skilleter 2007; Benkendorff *et al.* 2008). The information required to properly conserve populations of marine invertebrates is, however, often lacking (Edgar *et al.* 2005).

Information about the habitat requirements of under-boulder chitons is needed in particular, to increase our understanding of these little-understood molluscs. This has been highlighted by studies that have documented patterns of distribution among boulders indicative of aggregation (Chapman 2002; Grayson and Chapman 2004; Chapman 2005). All the models tested to account for the aggregation have failed to identify any aspects of their habitat that may be involved. It is possible that rock type is a feature of habitat that contributes to patterns of aggregation. For example, boulder-fields contain many discrete microhabitats (Le Hir and Hily 2005), and it is possible that the quality of these microhabitats will vary among boulder-fields with differing structure associated with rock type. In recent years it has become more common for studies to investigate chitons in intertidal boulder-field habitat, for example, studies of colonisation of assemblages including chitons onto artificial boulders (Chapman 2007, 2011), but these have all involved addition of artificial boulders of only one rock type. Information about the influence of rock type on patterns of chiton distribution would contribute to our understanding of the habitat requirements of these species in boulder-fields.

The aim of this study was to make observations of patterns of chiton distribution in boulder-fields on the Fleurieu Peninsula and Kangaroo Island in South Australia, where a particularly great diversity of chitons is known to occur (Cotton 1964; Kangas and Shepherd 1984). The habitat requirements of chitons were investigated by testing the hypotheses that the assemblages, abundances, and numbers of species of chitons would differ between boulder-fields comprising rock types of differing categories of hardness. To determine if the rock type of boulder-fields may influence patterns of distribution (e.g., aggregation) of chitons among boulders, the hypothesis was tested that chiton distribution frequencies would differ between the boulder-field types.

## Methods

Five intertidal boulder-fields were sampled along the coast of the Fleurieu Peninsula and five on Kangaroo Island in South Australia (Fig. 1) between October to December 2006. Depending on the make up of the boulders, boulder-fields were categorised into soft rock and

hard rock sites (Fig. 1). Soft rock boulders generally consisted of loosely-consolidated limestone, which was highly friable, in some cases to the extent that pieces could be broken by hand (indentation hardness <4 on Moh's hardness scale; Tabor 1954). They were often irregularly shaped with a rough, uneven surface. Hard-rock boulders were mostly ovoid in shape, and consisted of igneous or metamorphic rock such as basalt, granite, and quartzite, which was much smoother and less porous. Hard rock encompasses all rock types with an indentation hardness >4 on Moh's hardness scale (Tabor 1954). Sampling was done during low tides within an area at each site of 30m alongshore x 5m perpendicular to the shore, positioned so that the furthest point downshore was as far as possible into the shallow subtidal zone. At each site, a one hour timed-search survey was done (Benkendorff and Davis 2002), starting approximately one hour before low tide. The number and identities of all readily observable (>3mm) chitons present were recorded for each occupied boulder overturned, with the clock stopped during data recording. Similar numbers of boulders were able to be sampled during the timed-search between the two boulder-field types. Most species were able to be identified in the field, but some uncommon species were collected and identified according to (Cotton 1964). In most cases, *Ischnochiton elongatus* (Blainville, 1825) and *I. variegatus* (Adams and Angas, 1864) were unable to be reliably differentiated in the field and were therefore grouped under a single taxon, except when *I. variegatus* occurred as a distinctive brown morph, in which case it was recorded separately.

<FIGURE 1 ABOUT HERE>

Multivariate data of chiton assemblages were compared between the two types of boulder-fields (fixed factor), and between sites from the two geographical areas (Fleurieu Peninsula and Kangaroo Island; random factor), using two-way permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities using the PRIMER v6 software package (Plymouth Marine Laboratory, UK). Unrestricted permutations were done of raw data, which were square-root transformed prior to analysis to increase contributions of less common species (Anderson *et al.* 2008). Differences between assemblages were visualised on nMDS (non-metric multi-dimensional scaling) plots, and SIMPER (Similarity Percentages) was used to determine which species made the greatest contributions to any differences. Although many of the chiton species we encountered were very common, a range of uncommon species was also found. To investigate specifically how these uncommon species may be affected by rock type, an additional PERMANOVA analysis was done using

the same assemblage data and methods of analysis as for the main analysis, except that the data were transformed to presence/absence. In addition to these multivariate analyses, univariate data of overall abundances of chitons and species richness were also compared between hard and soft rock boulder-fields using two-way permutational ANOVA with Euclidean distance as the basis of the analyses.

Although the sites with different rock type were generally interspersed (Fig. 1), it is possible that wave exposure could vary between sites with different rock types. So to provide estimations of wave exposure at each site, the Baardseth's index was used (Baardseth 1970). This method uses the radial exposure of sites to a 7.5km fetch as an index of wave exposure, and has been used effectively in previous research of effects of wave exposure in South Australia (Wernberg and Connell 2008). Measurements were made on marine charts of 1:50,000 scale by placing a disc over each site with a radius corresponding to 7.5km, and counting the number of 10° sectors that did not include any obstructions (values can range from 0: fully sheltered, to 36: fully exposed). These values were then compared between hard and soft rock sites using one-way ANOVA. The measurements were also compared among sites with different chiton species richness and abundance using linear regression, to determine if patterns of chiton diversity and abundance may be related to wave exposure.

Chitons were often observed being aggregated on a small proportion of boulders within the boulder-fields, which is a pattern that may be influenced by rock type. This possibility was investigated by testing for non-random frequencies of the numbers of boulders with given numbers of chitons, done separately for Fleurieu Peninsula and Kangaroo Island using all boulders summed across boulder-fields of respective rock types. Using one-sample Kolmogorov-Smirnov tests in SPSS, comparisons were made between actual distributions and simulated Poisson distributions (which would be expected if chitons are randomly distributed among boulders). These analyses were done on *I. elongatus/variegatus* and *I. cariosus* (Pilsbry, 1892), which each had sufficiently large abundances for the analysis. Frequency distributions were also compared directly between different rock types by using two-sample Kolmogorov-Smirnov tests, which determined if the summed frequency distributions differed between reefs of hard vs soft rock type. Two separate tests were done for boulder-fields in the two geographical areas for *I. elongatus/variegatus* and *I. cariosus*.

## Results

A total of 22 chiton species was encountered across both areas (Table 2), with a range of 4-11 species per site (Fig. 1). Twenty one species were recorded at sites on Kangaroo Island and 15 on the Fleurieu Peninsula. Some species were very common, especially *Ischnochiton elongatus/variegatus* and *I. australis* (Sowerby, 1841), which accounted for two thirds of all individuals found. Other species were much rarer (see Table 2); five species occurred in such limited abundances that fewer than six individuals were found, with two of those species being represented by only a single individual.

There was much variation in assemblage composition between sites, but significantly different assemblages were found between hard and soft rock sites and this was consistent between the two areas (Table 3, Fig. 2). SIMPER revealed that the different assemblages between hard and soft rock sites were mostly the result of some common species having greater mean abundances in the hard rock boulder-fields (Table 2). *I. australis* in particular contributed to this pattern, because it was never observed in soft rock boulder-fields, and also *I. smaragdinus* (Angas, 1867), which was occasionally found in soft rock boulder-fields, but had greater abundances in those of hard rock. When the assemblage data were transformed to presence/absence, the significant difference between rock types no longer occurred ($F_{(1, 7)}$ = 2.19, $P > 0.05$) indicating that the assemblages of uncommon species were largely similar between the two types of boulder-fields. The mean total abundances of chitons from all species pooled were approximately three times greater in hard rock than in soft rock boulder-fields ($P < 0.05$, Table 3, Fig. 3a). However, the mean number of chiton species was similar between boulder-fields comprising the two rock types ($P > 0.05$, Table 3, Fig. 3b).

Wave exposure at the specific sites within intertidal reefs that were surveyed for chitons varied from fully sheltered (0) at Vivonne Bay to partly exposed at Port Willunga (7.5km wave fetch index = 10/36, Figure 1). However, on average, the wave exposure index did not differ significantly between the hard (6.6 ±3.1) and soft rock (4.2 ±3.2) sites (ANOVA, $F_{(1, 8)}$ = 1.44, $P > 0.25$). The linear regressions between wave exposure and the chiton assemblage variables were in neither case statistically significant (species richness $R^2 = 0.14$, $P > 0.25$; abundance $R^2 = 0.01$, $P > 0.75$).

<TABLE 2 ABOUT HERE>

<TABLE 3 ABOUT HERE>

<FIGURE 2 ABOUT HERE>

<FIGURE 3 ABOUT HERE>

On the Fleurieu Peninsula, *I. elongatus/variegatus* was non-randomly distributed among boulders from hard rock sites (Kolmogarov-Smirnov test statistic $D = 0.28$, $P < 0.001$), which appeared to be the result of a small proportion of boulders harbouring particularly high chiton abundances (9-12 individuals; Fig 4a). These aggregations were not observed on boulders from soft rock sites, where the species distribution was not significantly different to a random Poisson distribution ($D = 0.15$, $P > 0.25$, Fig. 4a). Conversely, on Kangaroo Island, non-random distributions were found for boulders from soft rock ($D = 0.22$, $P < 0.001$, Fig. 4b), but not those from hard rock sites ($D = 0.09$, $P > 0.5$, Fig. 4b). *I. cariosus* showed the reverse pattern for non-random distribution across rock types and geographical areas when compared to *I. elongatus/variegatus*. On the Fleurieu Peninsula, *I. cariosus* distributions were significantly different to the Poisson distribution on soft rocks ($D = 0.28$, $P < 0.05$, Fig. 4c), while on Kangaroo Island, a non-random distribution was found on hard rocks ($D = 0.24$, $P < 0.05$, Fig. 4d).

The two-sample Kolmogorov-Smirnov test of equality of distributions found significant differences between distributions of *I. elongatus/variegatus* from hard vs soft rock sites on Fleurieu Peninsula ($D = 0.31$, $P < 0.025$, Fig. 4a), perhaps because of the varying degree of aggregation between boulders from the two rock types. This outcome did not occur for the same test of *I. elongatus/variegatus* distributions from Kangaroo Island ($D = 0.13$, $P > 0.5$, Fig. 4b). In neither area did the distributions of *I. cariosus* differ significantly between boulders from hard vs soft rock sites (Fleurieu Peninsula $D = 0.1$, $P > 0.99$, Fig. 4c; Kangaroo Island $D = 0.1$, $P > 0.99$, Fig. 4d).

<FIGURE 4 ABOUT HERE>

**Discussion**

Observations of patterns of distribution and abundance of species are the logical first steps required to determine the processes and mechanisms that structure communities (Underwood *et al.* 2000). Several other studies have made large-scale observations of species distribution and abundance in boulder-fields (Grayson and Chapman 2004; Chapman 2005; Smoothey and Chapman 2007; Palmer 2011), but none have distinguished between types of boulder-fields that may differ in structure, geographical location, or in other ways. Our observations provide some clues about the habitat requirements and other aspects that may be structuring chiton assemblages. Some mechanism(s) operating in hard rock sites appear to allow common species to thrive, particularly *Ischnochiton australis*, *I. elongatus/variegates* and *I. smaragdinus*. These species were the main contributors to the pattern of greater overall abundance of chitons in hard rock sites. A group of less common species were also observed predominantly in the hard rock sites. Common species also occurred in soft rock sites, but in lesser abundances, along with a range of uncommon species, similar to that found in the hard rock sites. The results indicate that while the numbers of species did not differ between the two types of boulder-fields, the assemblage composition and total abundance did.

Although these surveys were only done at a single time, previous research has shown that the biodiversity of intertidal reef invertebrates is generally well represented in counts made using single standardised timed search surveys by experienced researchers (Benkendorff and Davis 2002, Benkendorff 2003, Gladstone, 2002). For example, observations of the occurrence of chiton species at one of the sites in this study (Myponga Beach) have been made repeatedly between 2001 and 2006 (K. Liversage, unpublished data), and during this time twelve species have been found, only two more than were found within the one hour timed search survey used in this study. Also, previous research into under-boulder chitons, in eastern Australia, through time (Smith and Otway 1997) has found no evidence that significant fluctuations occur. Smith and Otway (1997) reported reoccurrence for many of the same species we found, so assuming populations of these species act similarly in South Australia, the abundances we reported should represent those that generally occur at these sites, at least during the summer season.

The association between specific mollusc assemblages and rock type found in our results, and in other studies of intertidal reefs (Table 1), suggests that rock type may be a mechanism that influences the distribution of benthic molluscs such as chitons. Previous studies have found associations between sessile species and different rock types of intertidal boulders

(McGuinness and Underwood 1986; James and Underwood 1994), but no association was found when mobile species were similarly examined (McGuinness and Underwood 1986). The mobile species that have been included in studies of effects of rock type have, however, typically been habitat generalists (e.g. urchins or molluscs that inhabit numerous habitat types; McGuinness and Underwood 1986; Bavestrello *et al.* 2000) or species that do not live in close contact with the substratum (e.g. fish; Guidetti *et al.* 2004). All the chitons recorded in our study are habitat specialists that constantly rely on specific areas on rocks as substrata for adherence and grazing/feeding (Kangas and Shepherd 1984), and for protection from predation (Shepherd and Clarkson 2001). Stronger relationships between specific rock types and abundances of mobile species may be found if more studies investigate habitat specialists such as under-boulder chitons.

There did not appear to be any consistent relationship between the rock type of boulder-fields and the patterns of distribution of chitons among boulders within the boulder-fields. In some cases chitons were observed to have significantly non-random, overdispersed distributions among boulders, but this pattern occurred less than could be expected from the results of similar analyses of chiton distribution in New South Wales (Chapman 2002; Grayson and Chapman 2004; Chapman 2005). Rock type was associated with differing distribution frequencies of *I. elongatus/variegatus* in one area, suggesting that in some cases rock type may be influencing patterns of chiton aggregation, but the association was not spatially consistent. Overall, it appears that there is much variation in patterns of chiton distribution among boulders in South Australia.

Previous studies have shown that the degree of exposure of coastal sites to a 7.5km fetch is an effective method of estimating wave exposure, which can in turn influence the assemblage structure of algae and sessile animals (Ruuskanen *et al.* 1999; Wernberg and Connell 2008). Using this method, we did not find any indication that variability in chiton species richness or abundance was influenced by wave exposure, or that the differences in chiton assemblage structure between rock types was confounded by wave exposure. It is likely that most of the variability among sites was the result of physical features that differ between the hard and soft rock types, such as rock surface heterogeneity, friability, porosity, colour, and heat retention. Previous studies have found, however, that if large-scale observations of associations between rock type and benthic species distribution are investigated manipulatively, the associations sometimes cannot be directly explained by differences in rock type (Caffey 1982;

McGuinness 1988). The association found in the present study may have been caused by factors other than rock type that differ between hard and soft rock boulder-fields. For example, although the sizes of boulders were similar between the two types of boulder-fields, the shapes of boulders did appear to differ, with hard rock boulders being more ovoid in shape. It also appeared that boulders in soft rock boulder-fields were more often stacked on top of each other. Differently shaped boulders and those arranged in different ways within boulder-fields are known to harbour different species assemblages (Takada 1999; Le Hir and Hily 2005) and may be a cause of patterns of chiton aggregation.

In addition, chitons may be indirectly affected by other species that are influenced by rock type. Most of the chiton species observed in this study were algal grazers (Kangas and Shepherd 1984) and the type of rock that intertidal boulders are made of can affect the growth of algae on the upperside of boulders (McGuinness and Underwood 1986), so variation in algal growth among rock types may influence chiton distribution. Furthermore, some under-boulder chitons that were found in this study consume sponges, bryozoans, and ascidians (particularly *Ischnochiton smaragdinus*; Kangas and Shepherd 1984) and these encrusting invertebrates may be affected by rock type. Previous research has shown that spirorbid tubeworms (a particularly common group of sessile species in under-boulder habitat) recruit more abundantly under boulders comprised of darker- compared to lighter-coloured rock types (James and Underwood 1994), and chitons may be influenced by variation in their abundances. One species of chiton in South Australia (*Lorica volvox*) is a specialist predator of spirorbid tubeworms (Kangas and Shepherd 1984), so factors affecting spirorbids may consequently affect this species. Also, many benthic molluscs that graze rock surfaces are influenced by rock surface heterogeneity (Chapman and Underwood 1994; Underwood 2004) and the masses of spirorbid worm tubes under boulders would likely increase surface heterogeneity considerably. It did appear that spirorbid abundances varied among the sites, so further manipulative experiments should be done to determine if the presence of spirorbids and/or other mechanisms cause the patterns found in this study.

In conclusion, observations of chiton assemblages in boulder-fields in South Australia suggest that rock type may be affecting their distributions. Greater abundances of common species were observed in boulder-fields comprising harder rock types such as granite, basalt, and quartzite and lower overall abundances occurred in boulder-fields comprised of soft limestone. In some cases, chitons in boulder-fields of different rock types also appear to have

distinct distributional patterns among boulders. It is thus clear that sites with different rock type need to be distinguished both during ecological investigations of specialist rocky intertidal species such as under-boulder chitons, and during conservation programmes aiming to protect intertidal species that are habitat specialists, such as those in boulder-fields.

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References

Addessi, L. (1994) Human disturbance and long-term changes on a rocky intertidal community. *Ecological Applications* 4, 786-797

Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, Plymouth

Baardseth, E.M. (1970) A square-scanning, two stage sampling method of estimating seaweed quantities. *Norwegian Institute of Seaweed Research* Report No. 33: 1-40

Banks, S.A. & Skilleter, G.A. (2007) The importance of incorporating fine-scale habitat data into the design of an intertidal marine reserve system. *Biological Conservation* 138, 13-29

Bavestrello, G., Bianchi, C.N., Calcinai, B., Cattaneo-Vietti, R., Cerrano, C., Morri, C., Puce, S. & Sara, M. (2000) Bio-mineralogy as a structuring factor for marine epibenthic communities. *Marine Ecology Progress Series* 193, 241-249

Benkendorff, K. (2003). Rapid biodiversity assessment on rocky intertidal reefs: An examination of molluscan species richness. *Records of the South Australian Museum Monograph Series* **7**, 67-78.

Benkendorff, K. & Davis, A.R. (2002) Identifying hotspots of molluscan species richness on rocky intertidal reefs. *Biodiversity and Conservation* 11, 1959-1973

Benkendorff, K. & Davis, A.R. (2004) Gastropod egg mass deposition on a temperate, wave-exposed coastline in New South Wales, Australia: implications for intertidal conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 263-280

Benkendorff, K., Fairweather, P.G. & Dittmann, S. (2008) Intertidal shores: life on the edge. In Shepherd S.A., Bryars S., Kirkegaard I., Harbison P. and Jennings J. (eds) Natural History of the Gulf St Vincent. Adelaide: Royal Society of South Australia, pp 121-131.

Berntsson, K.M., Jonsson, P.R., Lejhall, M. & Gatenholm, P. (2000) Analysis of behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology* 251, 59-83

Caffey, H.M. (1982) No effect of naturally-occurring rock types on settlement or survival in the intertidal barnacle, *Tesseropora rosea* (Krauss). *Journal of Experimental Marine Biology and Ecology* 63, 119-132

Chapman, M.G. (2002) Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecology* 27, 211-228

Chapman, M.G. (2005) Molluscs and echinoderms under boulders: Tests of generality of patterns of occurence. *Journal of Experimental Marine Biology and Ecology* 325, 65-83

Chapman, M.G. (2007) Colonization of novel habitat: Tests of generality of patterns in a diverse invertebrate assemblage. *Journal of Experimental Marine Biology and Ecology* 348, 97-110

Chapman, M.G. (2011) Restoring intertidal boulder-fields as habitat for "specialist" and "generalist" animals. *Restoration Ecology* 19, 1-9

Chapman, M.G. & Underwood, A.J. (1994) Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology* 179, 145-169

Cotton, B.C. (1964) South Australian mollusca; chitons, Govt. Printer, Adelaide

Davidson, R.J. & Chadderton, W.L. (1994) Marine reserve selection along the Abel Tasman National Park coast, New Zealand: consideration of subtidal rocky communities. *Aquatic Conservation: Freshwater and Marine Ecosystems* 4, 153-167

Edgar, G.J., Samson, C.R. & Barrett, N.S. (2005) Species extinction in the marine environment: Tasmania as a regional example of overlooked losses in biodiversity. *Conservation Biology* 19, 1294-1300

Erlandsson, J., Kostylev, V. & Williams, G.A. (1999) A field technique for estimating the influence of surface complexity on movement tortuosity in the tropical limpet *Cellana grata* Gould. *Ophelia* 50, 215-224

Fraser, C.M.L., Coleman, R.A. & Klein, J.C. (2010) Up or down? Limpet orientation on steeply sloped substrata. *Aquatic Biology* 11, 91-98

Garrity, S.D. & Levings, S.C. (1983) Homing to scars as a defence against predators in the Pulmonate limpet *Siphonaria gigas* (Gastropoda). *Marine Biology* 72, 319-324

Giesel, J.T. (1969) Factors influencing the growth and relative growth of *Acmaea Digitalis*, a limpet. *Ecology* 50, 1084-1087

Gladstone, W. (2002) The potential value of indicator groups in the selection of marine reserves. *Biological Conservation* 104, 211-220.

Gosselin, L.A. & Bourget, E. (1989) The performance of an intertidal predator Thais lapillus, in relation to structural heterogeneity. *Journal of Animal Ecology* 58, 287-303

Grayson, J.E. & Chapman, M.G. (2004) Patterns of distribution and abundance of chitons of the genus *Ischnochiton* in intertidal boulder fields. *Austral Ecology* 29, 363-373

Grenon, J.F. & Walker, G. (1981) The tenacity of the limpet, *Patella vulgata* L.: An experimental approach. *Journal of Experimental Marine Biology and Ecology* 54, 277-308

Guidetti, P., Bianchi, C.N., Chiantore, M., Schiaparelli, S., Morri, C. & Cattaneo-Vietti, R. (2004) Living on the rocks: substrate mineralogy and the structure of subtidal rocky substrate communities in the Mediterranean Sea. *Marine Ecology Progress Series* 274, 57-68

Herbert, R.J.H. & Hawkins, S.J. (2006) Effect of rock type on the recruitment and early mortality of the barnacle *Chthamalus montagui*. *Journal of Experimental Marine Biology and Ecology* 334, 96-108

James, R.J. & Underwood, A.J. (1994) Influence of colour of substratum on recruitment of spirorbid tubeworms to different types of intertidal boulders. *Journal of Experimental Marine Biology and Ecology* 181, 105-115

Kangas, M. & Shepherd, S.A. (1984) Distribution and feeding of chitons in a boulder habitat at West Island, South Australia. *Journal of the Malacological Society of Australia* 6, 101-111

Kohler, J., Hansen, P.D. & Wahl, M. (1999) Colonization patterns at the substratum-water interface: how does surface microtopography influence recruitment patterns of sessile organisms? *Biofouling* 14, 237-248

Le Hir, M. & Hily, C. (2002) First observations in a high rocky-shore communty after the *Erika* oil spill (December 1999, Brittany, France). *Marine Pollution Bulletin* 44, 1243-1252

Le Hir, M. & Hily, C. (2005) Macrofaunal diversity and habitat structure in intertidal boulder fields. *Biodiversity and Conservation* 14, 233-250

Le Tourneux, F. & Bourget, E. (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. *Marine Biology* 97, 57-66

McGuinness, K.A. (1988) Explaining patterns in abundances of organisms on boulders: the failure of 'natural experiments'. *Marine Ecology Progress Series* 48, 199-204

McGuinness, K.A. & Underwood, A.J. (1986) Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology* 104, 97-123

Moreira, J. (2006) Patterns of occurrence of grazing molluscs on sandstone and concrete seawalls in Sydney Harbour (Australia). *Molluscan Research* 26, 51-60

O'Hara, T.D. (2002) Endemism, rarity and vulnerability of marine species along a temperate coastline. *Invertebrate Systematics* 16, 671-684

Palmer, A.N.S. (2011) Spatial and genetic investigation of aggregation in *Ischnochiton* (Polyplacophora; Neoloricata; Ischnochitonina; Ischnochitonidae; Ischnochitoninae) species with different larval development. *Austral Ecology* 37, 110-124

Ruuskanen, A., Bäck, S. & Reitalu, T. (1999) A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. *Marine Biology* 134, 139-145

Schiaparelli, S., Guidetti, P. & Cattaneo-Vietti, R. (2003) Can mineralogical features affect the distribution patterns of sessile gastropods? The Vermetidae case in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 83, 1267-1268

Shepherd, S.A. & Clarkson, P.S. (2001) Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus*. *Marine and Freshwater Research* 52, 311-322

Smith, K.A. & Otway, N.M. (1997) Spatial and temporal patterns of abundance and the effects of disturbance on under-boulder chitons. *Molluscan Research* 18, 43-57

Smoothey, A.F. & Chapman, M.G. (2007) Small-scale variability in the dispersion of the sea urchin *Heliocidaris erythrogramma* among boulders. *Marine Ecology Progress Series* 340, 89-99

Tabor, D. (1954) Hardness of Solids. *Endeavour* 13, 27-32

Takada, Y. (1999) Influence of shade and number of boulder layers on mobile organisms on a warm temperate boulder shore. *Marine Ecology Progress Series* 189, 171-179

Thompson, R.C., Crowe, T.P. & Hawkins, S.J. (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* 29, 168-191

Timoshkin, O.A., Suturin, A.N., Maximova, N.V., Semiturkina, N.A., Galkin, A.N., Kulikova, N.N., Khanaev, I.V. & Ropstörf, P. (2002) Rock preferences and microdistribution peculiarities of Porifera and Gastropoda in the shallow littoral zone of Lake Baikal (east Siberia) as evidenced by underwater macrophotograph analysis. *Berliner Paläobiologische Abhandlungen* 4, 193-200

Todd, C.D. & Turner, S.J. (1986) Ecology of intertidal and sublittoral cryptic epifaunal assemblages. I. Experimental rationale and the analysis of larval settlement. *Journal of Experimental Marine Biology and Ecology* 99, 199-231

Underwood, A.J. (2004) Landing on one's foot: small-scale topographic features of habitat and the dispersion of juvenile intertidal gastropods. *Marine Ecology Progress Series* 268, 173-182

Underwood, A.J., Chapman, M.G. & Connell, S.D. (2000) Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250, 97-115

Vermeij, G.J. (1971) Substratum relationships of some tropical Pacific intertidal gastropods. *Marine Biology* 10, 315-320

Wernberg, T., Connell, S.D. (2008) Physical disturbance and subtidal habitat structure on open rocky coasts: Effects of wave exposure, extent and intensity. *Journal of Sea Research* 59, 237-248

**TABLE 1: Previous studies on effects of rock type on benthic molluscs in aquatic habitats**

| Study | Habitat | Region | Rock types included | Molluscs affected by rock type |
|---|---|---|---|---|
| McGuinness and Underwood (1986) | intertidal boulders | south-eastern Australia | sandstone, shale | none (6 gastropods were tested) |
| Davidson and Chadderton (1994) | subtidal and intertidal rocky benthos | New Zealand | granite, limestone | limpets (Nacellidae), turban snails (Turbinidae), top snails (Trochidae) |
| Bavestrello *et al.* (2000) | subtidal rocky benthos | north-west Mediterranean | quartzite, sandstone, marl limestone, puddingstone, limestone, limestone-dolomite | worm snails (Vermetidae) |
| Timoshkin *et al.* (2002) | freshwater lake rocky benthos | Lake Baikal (east Siberia) | granitoids, amphibolite | unspecified gastropods |
| Schiaparelli *et al.* (2003) | shallow-subtidal and intertidal rocky benthos | north-eastern Sardinia | granite, limestone | worm snails (Vermetidae) |
| Moreira (2006) | artificial sea walls | Sydney Harbour (south-eastern Australia) | sandstone, concrete | limpets (Nacellidae, Lottiidae, Siphonariidae), periwinkles (Littorinidae) |
| This study | intertidal boulders | South Australia | limestone, quartzite/granite/basalt | chitons (Polyplacophora) |

**TABLE 2:** Contributions of chiton species to measures of dissimilarity, calculated in PRIMER v6, between assemblages at five soft rock and five hard rock sites (Fig. 1). All species that were found are displayed, in order of their relative contribution to dissimilarity.

| Species | Mean abundance | | Ratio diss/SD | % Contribution |
|---|---|---|---|---|
| | Soft rock boulder-fields | Hard rock boulder-fields | | |
| *Ischnochiton australis* (Sowerby, 1840) | 0 | 103.2 | 0.95 | 34.68 |
| *Ischnochiton elongatus* (Blainville, 1825) */variegatus* (H. Adams & Angas, 1864) | 66.6 | 103.2 | 1.17 | 19.52 |
| *Ischnochiton smaragdinus* (Angas, 1867) | 0.6 | 35.0 | 1.02 | 14.83 |
| *Ischnochiton cariosus* (Pilsbry, 1892) | 17.2 | 32.6 | 1.01 | 14.35 |
| *Ischnochiton variegatus* (brown morph; H. Adams & Angas, 1864) | 8.8 | 0.0 | 0.62 | 3.24 |
| *Cryptoplax striata* (Lamarck, 1819) | 5.0 | 0.0 | 0.97 | 1.89 |
| *Ischnochiton virgatus* (Reeve, 1848) | 1.0 | 5.2 | 0.81 | 1.75 |
| *Ischnochiton lineolatus* (de Blainville, 1825 | 3.4 | 4.2 | 1.23 | 1.57 |
| *Ischnochiton thomasi* (Bednall, 1897) | 0.2 | 3.0 | 0.82 | 1.38 |
| *Craspedoplax variabilis* (Adams & Angas, 1864) | 2.2 | 0.6 | 0.58 | 1.32 |
| *Ischnochiton* contractus (Reeve, 1847) | 2.6 | 0.0 | 0.71 | 1.02 |
| *Ischnochiton torri* (Iredale & May, 1916) | 1.0 | 1.6 | 1.10 | 0.87 |
| *Lorica volvox* (Reeve, 1847) | 2.0 | 0.2 | 0.55 | 0.84 |
| *Chiton diaphorus* (Iredale & May, 1916) | 0.0 | 2.0 | 0.88 | 0.83 |
| *Chiton jugosus* (Gould, 1846) | 1.0 | 0.8 | 0.67 | 0.67 |
| *Acanthochitona bednalli* (Pilsbry, 1894) | 0.4 | 0.4 | 0.95 | 0.28 |
| *Callochiton crocinus* (Reeve, 1847) | 0.4 | 0.4 | 0.86 | 0.28 |
| *Chiton tricostalis* (Pilsbry, 1894) | 0.6 | 0.0 | 0.48 | 0.27 |
| *Callistochiton antiquus* (Reeve, 1847) | 0.4 | 0.0 | 0.77 | 0.17 |
| *Bassethullia matthewsi* (Bednall & Pilsbry, 1894) | 0.0 | 0.2 | 0.48 | 0.10 |
| *Acanthochitona sueurii* (de Blainville, 1825) | 0.2 | 0.0 | 0.48 | 0.08 |
| *Leptochiton matthewsianus* (Bednall, 1906) | 0.2 | 0.0 | 0.48 | 0.07 |

**TABLE 3:** Permutational ANOVA on multivariate data of chiton assemblage composition, and univariate data of chiton abundance and number of chiton species, between hard rock and soft rock boulder-fields. Assemblage composition data were square-root transformed prior to analysis to increase the contribution of less common species. When the *P*-values of the interaction term were >0.25, they were pooled with the residual to provide a more powerful test for the relevant null hypotheses (Underwood 1997), ***P* < 0.01.

| | | **Assemblage composition** | | **Abundance** | | **Number of species** | |
|---|---|---|---|---|---|---|---|
| | df | MS | F | MS | F | MS | F |
| Rock type | 1 | 3696 | 2.86** | 89939 | 12.40** | 7.35 | 2.16 |
| Geographical area | 1 | 1479 | 1.14 | 13113 | 1.81 | 7.35 | 2.16 |
| Ro x Ge† | 1 | 1570 | | 2815 | | 0.004 | |
| Residual | 6 | 1247 | | 7996 | | 3.97 | |
| Pooled | 7 | 1293 | | 7256 | | 3.41 | |

†Term pooled with residual

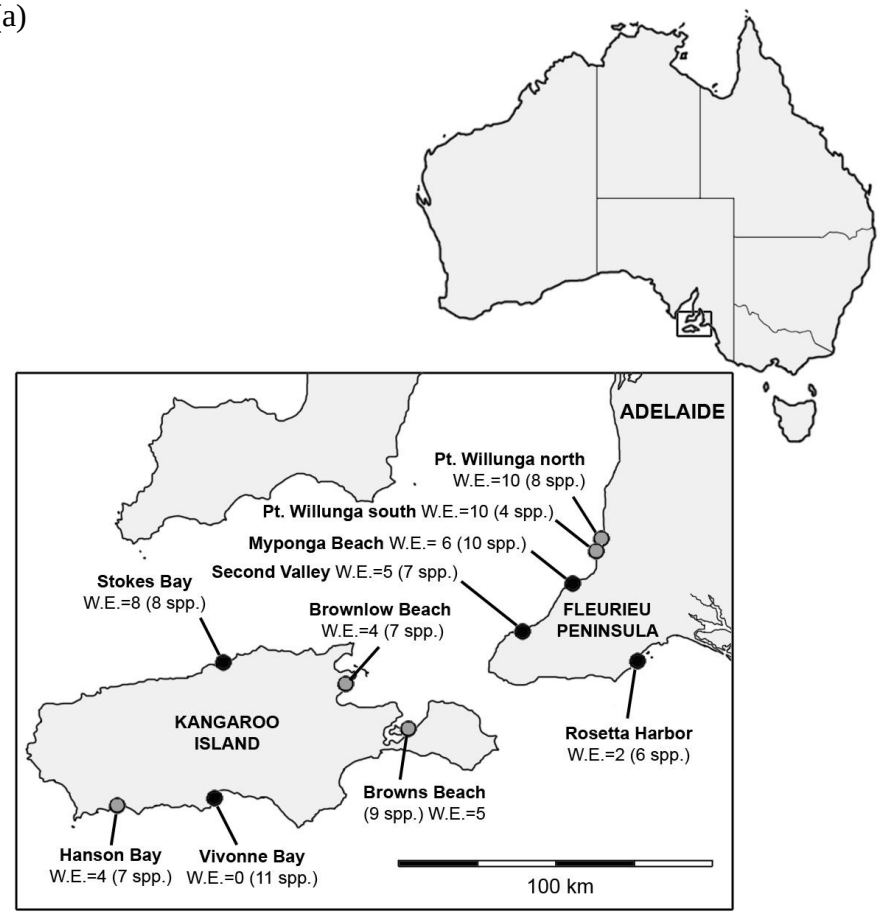
**FIGURE 1:** Intertidal boulder fields surveyed for chitons showing a) the geographical location along the coast of South Australia and representative study sites at b) Port Willunga (soft rock) and c) Vivonne Bay (hard rock). In the map (a), sites indicated by black symbols are hard rock boulder-fields; those indicated by grey symbols are soft rock. Also displayed for each site is the index of wave exposure (W.E.) from a 7.5km fetch, which can range from 0 (fully sheltered) to 36 (fully exposed). This index is calculated for the specific area of boulder habitat that was surveyed for chitons at each site in this study, and is not necessarily indicative of exposure across the whole reef based on orientation and openness. The total numbers of chiton species found at each site are specified in parentheses.

**FIGURE 2:** nMDS ordination of chiton assemblages (species abundance square root transformed) found during one hour timed search surveys in boulder-fields that were in Fleurieu Peninsula and hard rock (▲), in Fleurieu Peninsula and soft rock (△), in Kangaroo Island and hard rock ( ● ), and in Kangaroo Island and soft rock ( ○ ).

**FIGURE 3:** Differences in mean (± S.E.) (a) abundance and (b) number of species of chitons found during one hour time search surveys in boulder-fields comprised of hard and soft rock types. Both measures were statistically similar among sites in Fleurieu Peninsula and Kangaroo Island, data shown are means of the sites across the two areas.

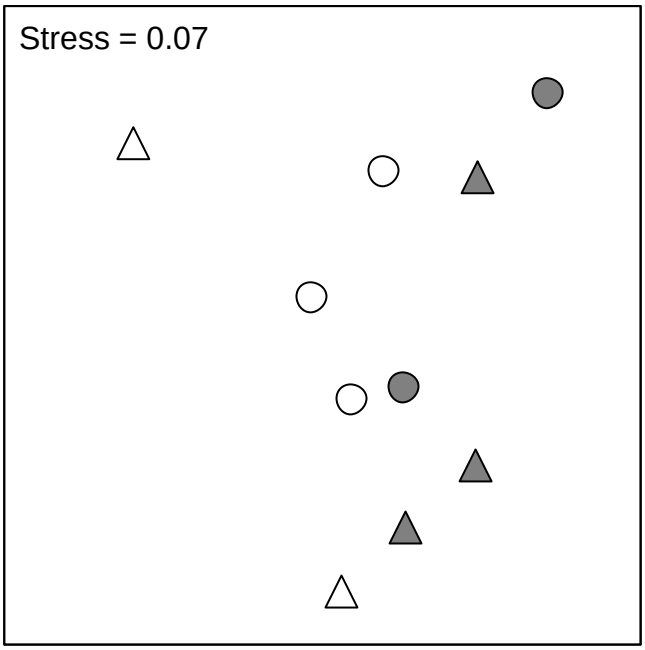
**FIGURE 4:** Frequency distributions of chitons across boulders in sites of hard rock ( ■ ) and soft rock ( ▩ ) for (a) *Ischnochiton elongatus/variegatus* in Fleurieu Peninsula, (b) *I. elongatus/variegatus* in Kangaroo Island, (c) *I. cariosus* in Fleurieu Peninsula, and (d) *I. cariosus* in Kangaroo Island; * One-sample Kolmogorov-Smirnov test of non-random distribution for boulders from hard rock sites $P < 0.05$; ** One-sample Kolmogorov-Smirnov test, soft rock sites $P < 0.05$; *** Two-sample Kolmogorov-Smirnov test comparing distributions from hard vs soft rock sites $P < 0.05$.

(a)


ADELAIDE
Pt. Willunga north
W.E.=10 (8 spp.)
Pt. Willunga south W.E.=10 (4 spp.)
Myponga Beach W.E.= 6 (10 spp.)
Second Valley W.E.=5 (7 spp.)
Stokes Bay
W.E.=8 (8 spp.)
Brownlow Beach
W.E.=4 (7 spp.)
FLEURIEU
PENINSULA
KANGAROO
ISLAND
Rosetta Harbor
W.E.=2 (6 spp.)
Browns Beach
(9 spp.) W.E.=5
Hanson Bay
W.E.=4 (7 spp.)
Vivonne Bay
W.E.=0 (11 spp.)
100 km

(b)

(c)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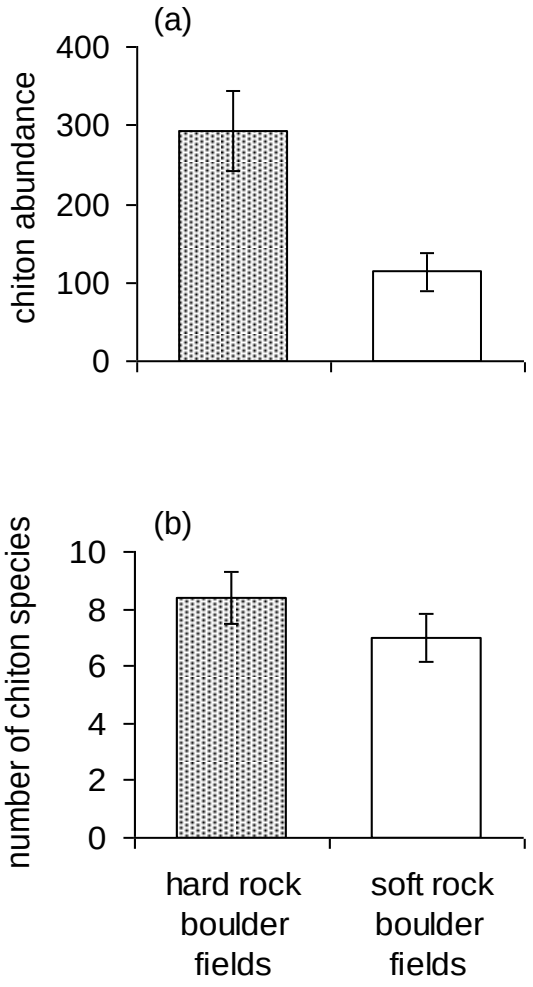
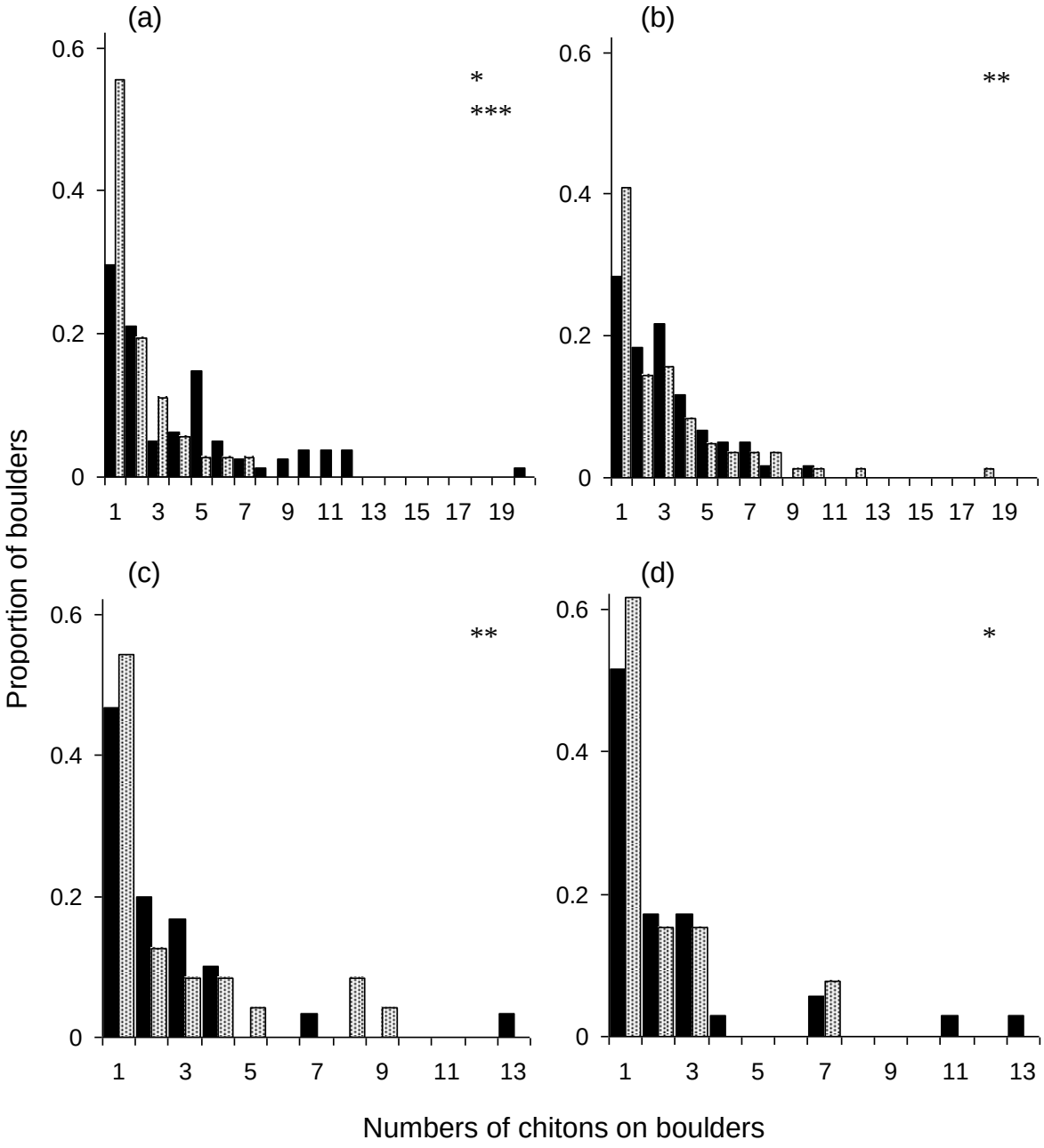

(a)
chiton abundance
400
300
200
100
0
(b)
number of chiton species
10
8
6
4
2
0
hard rock boulder fields
soft rock boulder fields


(a)
(b)
(c)
(d)
*
***
**
**
*
0.6
0.4
0.2
0
1 3 5 7 9 11 13 15 17 19
1 3 5 7 9 11 13
Proportion of boulders
Numbers of chitons on boulders