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

3

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

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35 **Abstract**

36

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

53

54

55 **Introduction**

56

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

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

79

80 <TABLE 1 ABOUT HERE>

81

82 A particularly wide range of mollusc species occur in the habitats on intertidal boulders.
83 When moveable rocks are present in the intertidal zone, a range of mobile and sessile species
84 are often found on the upper- and under-sides of the rocks (McGuinness and Underwood
85 1986; Todd and Turner 1986; Chapman 2007) and on the underlying substratum (Todd and
86 Turner 1986). Sometimes intertidal boulders occur on their own (e.g. within small rock
87 pools), but most often they are clustered together on patches of shore called ‘boulder-fields’,
88 that can be a few or many square metres in area.

89

90 Some species in boulder-fields are also commonly found in other intertidal habitats (e.g.
91 snails and limpets that occur on upsides of boulders, and also on stable rock platforms;
92 McGuinness and Underwood 1986), while others appear to be boulder-field specialists, and
93 are rarely found elsewhere (Kangas and Shepherd 1984; Chapman 2011). This is particularly
94 the case for a range of chitons (Polyplacophora: Mollusca) that are found almost exclusively
95 underneath boulders, where they are at less risk from predation (Shepherd and Clarkson
96 2001). Some species of under-boulder chitons are rare and considered threatened. For
97 example, the documented extent of distribution for one species, *Bassethullia* (Pilsbury, 1928)
98 *glypta* (Sykes, 1896), is confined to a small area at the entrances of two bays in south eastern
99 Australia (O'Hara 2002). The rarity and endemism of many species in boulder-fields, and the
100 susceptibility of the habitat to disturbance (e.g., Addessi 1994; Le Hir and Hily 2002), has led
101 to an increasing number of authors acknowledging that the habitat requires priority in coastal
102 conservation programmes (Thompson *et al.* 2002; Benkendorff and Davis 2004; Banks and

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

105
106 Information about the habitat requirements of under-boulder chitons is needed in particular, to
107 increase our understanding of these little-understood molluscs. This has been highlighted by
108 studies that have documented patterns of distribution among boulders indicative of
109 aggregation (Chapman 2002; Grayson and Chapman 2004; Chapman 2005). All the models
110 tested to account for the aggregation have failed to identify any aspects of their habitat that
111 may be involved. It is possible that rock type is a feature of habitat that contributes to patterns
112 of aggregation. For example, boulder-fields contain many discrete microhabitats (Le Hir and
113 Hily 2005), and it is possible that the quality of these microhabitats will vary among boulder-
114 fields with differing structure associated with rock type. In recent years it has become more
115 common for studies to investigate chitons in intertidal boulder-field habitat, for example,
116 studies of colonisation of assemblages including chitons onto artificial boulders (Chapman
117 2007, 2011), but these have all involved addition of artificial boulders of only one rock type.
118 Information about the influence of rock type on patterns of chiton distribution would
119 contribute to our understanding of the habitat requirements of these species in boulder-fields.

120
121 The aim of this study was to make observations of patterns of chiton distribution in boulder-
122 fields on the Fleurieu Peninsula and Kangaroo Island in South Australia, where a particularly
123 great diversity of chitons is known to occur (Cotton 1964; Kangas and Shepherd 1984). The
124 habitat requirements of chitons were investigated by testing the hypotheses that the
125 assemblages, abundances, and numbers of species of chitons would differ between boulder-
126 fields comprising rock types of differing categories of hardness. To determine if the rock type
127 of boulder-fields may influence patterns of distribution (e.g., aggregation) of chitons among
128 boulders, the hypothesis was tested that chiton distribution frequencies would differ between
129 the boulder-field types.

130

131

132 **Methods**

133

134 Five intertidal boulder-fields were sampled along the coast of the Fleurieu Peninsula and five
135 on Kangaroo Island in South Australia (Fig. 1) between October to December 2006.

136 Depending on the make up of the boulders, boulder-fields were categorised into soft rock and

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

156

157 <FIGURE 1 ABOUT HERE>

158

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

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

176

177 Although the sites with different rock type were generally interspersed (Fig. 1), it is possible
178 that wave exposure could vary between sites with different rock types. So to provide
179 estimations of wave exposure at each site, the Baardseth's index was used (Baardseth 1970).
180 This method uses the radial exposure of sites to a 7.5km fetch as an index of wave exposure,
181 and has been used effectively in previous research of effects of wave exposure in South
182 Australia (Wernberg and Connell 2008). Measurements were made on marine charts of
183 1:50,000 scale by placing a disc over each site with a radius corresponding to 7.5km, and
184 counting the number of 10° sectors that did not include any obstructions (values can range
185 from 0: fully sheltered, to 36: fully exposed). These values were then compared between hard
186 and soft rock sites using one-way ANOVA. The measurements were also compared among
187 sites with different chiton species richness and abundance using linear regression, to
188 determine if patterns of chiton diversity and abundance may be related to wave exposure.

189

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

203

204

205 **Results**

206

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

214

215 There was much variation in assemblage composition between sites, but significantly
216 different assemblages were found between hard and soft rock sites and this was consistent
217 between the two areas (Table 3, Fig. 2). SIMPER revealed that the different assemblages
218 between hard and soft rock sites were mostly the result of some common species having
219 greater mean abundances in the hard rock boulder-fields (Table 2). *I. australis* in particular
220 contributed to this pattern, because it was never observed in soft rock boulder-fields, and also
221 *I. smaragdinus* (Angas, 1867), which was occasionally found in soft rock boulder-fields, but
222 had greater abundances in those of hard rock. When the assemblage data were transformed to
223 presence/absence, the significant difference between rock types no longer occurred ($F_{(1, 7)} =$
224 $2.19, P > 0.05$) indicating that the assemblages of uncommon species were largely similar
225 between the two types of boulder-fields. The mean total abundances of chitons from all
226 species pooled were approximately three times greater in hard rock than in soft rock boulder-
227 fields ($P < 0.05$, Table 3, Fig. 3a). However, the mean number of chiton species was similar
228 between boulder-fields comprising the two rock types ($P > 0.05$, Table 3, Fig. 3b).

229

230 Wave exposure at the specific sites within intertidal reefs that were surveyed for chitons
231 varied from fully sheltered (0) at Vivonne Bay to partly exposed at Port Willunga (7.5km
232 wave fetch index = 10/36, Figure 1). However, on average, the wave exposure index did not
233 differ significantly between the hard (6.6 ± 3.1) and soft rock (4.2 ± 3.2) sites (ANOVA, $F_{(1, 8)}$
234 $= 1.44, P > 0.25$). The linear regressions between wave exposure and the chiton assemblage
235 variables were in neither case statistically significant (species richness $R^2 = 0.14, P > 0.25$;
236 abundance $R^2 = 0.01, P > 0.75$).

237

238 <TABLE 2 ABOUT HERE>

239

240 <TABLE 3 ABOUT HERE>

241

242 <FIGURE 2 ABOUT HERE>

243

244 <FIGURE 3 ABOUT HERE>

245

246 On the Fleurieu Peninsula, *I. elongatus/variegatus* was non-randomly distributed among
247 boulders from hard rock sites (Kolmogorov-Smirnov test statistic $D = 0.28$, $P < 0.001$), which
248 appeared to be the result of a small proportion of boulders harbouring particularly high chiton
249 abundances (9-12 individuals; Fig 4a). These aggregations were not observed on boulders
250 from soft rock sites, where the species distribution was not significantly different to a random
251 Poisson distribution ($D = 0.15$, $P > 0.25$, Fig. 4a). Conversely, on Kangaroo Island, non-
252 random distributions were found for boulders from soft rock ($D = 0.22$, $P < 0.001$, Fig. 4b),
253 but not those from hard rock sites ($D = 0.09$, $P > 0.5$, Fig. 4b). *I. cariosus* showed the reverse
254 pattern for non-random distribution across rock types and geographical areas when compared
255 to *I. elongatus/variegatus*. On the Fleurieu Peninsula, *I. cariosus* distributions were
256 significantly different to the Poisson distribution on soft rocks ($D = 0.28$, $P < 0.05$, Fig. 4c),
257 while on Kangaroo Island, a non-random distribution was found on hard rocks ($D = 0.24$, $P <$
258 0.05 , Fig. 4d).

259

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

268

269 <FIGURE 4 ABOUT HERE>

270

271 **Discussion**

272

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

288

289 Although these surveys were only done at a single time, previous research has shown that the
290 biodiversity of intertidal reef invertebrates is generally well represented in counts made using
291 single standardised timed search surveys by experienced researchers (Benkendorff and Davis
292 2002, Benkendorff 2003, Gladstone, 2002). For example, observations of the occurrence of
293 chiton species at one of the sites in this study (Myponga Beach) have been made repeatedly
294 between 2001 and 2006 (K. Liversage, unpublished data), and during this time twelve species
295 have been found, only two more than were found within the one hour timed search survey
296 used in this study. Also, previous research into under-boulder chitons, in eastern Australia,
297 through time (Smith and Otway 1997) has found no evidence that significant fluctuations
298 occur. Smith and Otway (1997) reported reoccurrence for many of the same species we found,
299 so assuming populations of these species act similarly in South Australia, the abundances we
300 reported should represent those that generally occur at these sites, at least during the summer
301 season.

302

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

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

318

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

329

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

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

349

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

369

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

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

379

380

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382

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535 open rocky coasts: Effects of wave exposure, extent and intensity. *Journal of Sea*
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1 **TABLE 1: Previous studies on effects of rock type on benthic molluscs in aquatic habitats**

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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 <i>et al.</i> (2000)	subtidal rocky benthos	north-west Mediterranean	quartzite, sandstone, marl limestone, puddingstone, limestone, limestone-dolomite	worm snails (Vermetidae)
Timoshkin <i>et al.</i> (2002)	freshwater lake rocky benthos	Lake Baikal (east Siberia)	granitoids, amphibolite	unspecified gastropods
Schiaparelli <i>et al.</i> (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)

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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	% Contribution	7
	Soft rock boulder-fields	Hard rock boulder-fields			
<i>Ischnochiton australis</i> (Sowerby, 1840)	0	103.2	0.95	34.68	10
<i>Ischnochiton elongatus</i> (Blainville, 1825)	66.6	103.2	1.17	19.52	11
<i>variegatus</i> (H. Adams & Angas, 1864)					
<i>Ischnochiton smaragdinus</i> (Angas, 1867)	0.6	35.0	1.02	14.83	12
<i>Ischnochiton cariosus</i> (Pilsbry, 1892)	17.2	32.6	1.01	14.35	13
<i>Ischnochiton variegatus</i> (brown morph; H. Adams & Angas, 1864)	8.8	0.0	0.62	3.24	14
<i>Cryptoplax striata</i> (Lamarck, 1819)	5.0	0.0	0.97	1.89	15
<i>Ischnochiton virgatus</i> (Reeve, 1848)	1.0	5.2	0.81	1.75	16
<i>Ischnochiton lineolatus</i> (de Blainville, 1825)	3.4	4.2	1.23	1.57	17
<i>Ischnochiton thomasi</i> (Bednall, 1897)	0.2	3.0	0.82	1.38	18
<i>Craspedoplax variabilis</i> (Adams & Angas, 1864)	2.2	0.6	0.58	1.32	19
<i>Ischnochiton contractus</i> (Reeve, 1847)	2.6	0.0	0.71	1.02	20
<i>Ischnochiton torri</i> (Iredale & May, 1916)	1.0	1.6	1.10	0.87	21
<i>Lorica volvox</i> (Reeve, 1847)	2.0	0.2	0.55	0.84	22
<i>Chiton diaphorus</i> (Iredale & May, 1916)	0.0	2.0	0.88	0.83	23
<i>Chiton jugosus</i> (Gould, 1846)	1.0	0.8	0.67	0.67	24
<i>Acanthochitona bednalli</i> (Pilsbry, 1894)	0.4	0.4	0.95	0.28	25
<i>Callochiton crocinus</i> (Reeve, 1847)	0.4	0.4	0.86	0.28	26
<i>Chiton tricostalis</i> (Pilsbry, 1894)	0.6	0.0	0.48	0.27	27
<i>Callistochiton antiquus</i> (Reeve, 1847)	0.4	0.0	0.77	0.17	28
<i>Bassethullia matthewsi</i> (Bednall & Pilsbry, 1894)	0.0	0.2	0.48	0.10	29
<i>Acanthochitona sueurii</i> (de Blainville, 1825)	0.2	0.0	0.48	0.08	30
<i>Leptochiton matthewsianus</i> (Bednall, 1906)	0.2	0.0	0.48	0.07	31

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

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	df	Assemblage composition		Abundance		Number of species	
		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	

42 [†]Term pooled with residual

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

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70 **FIGURE 2:** nMDS ordination of chiton assemblages (species abundance square root
 71 transformed) found during one hour timed search surveys in boulder-fields that were in
 72 Fleurieu Peninsula and hard rock (\blacktriangle), in Fleurieu Peninsula and soft rock (\triangle), in Kangaroo
 73 Island and hard rock (\bullet), and in Kangaroo Island and soft rock (\circ).

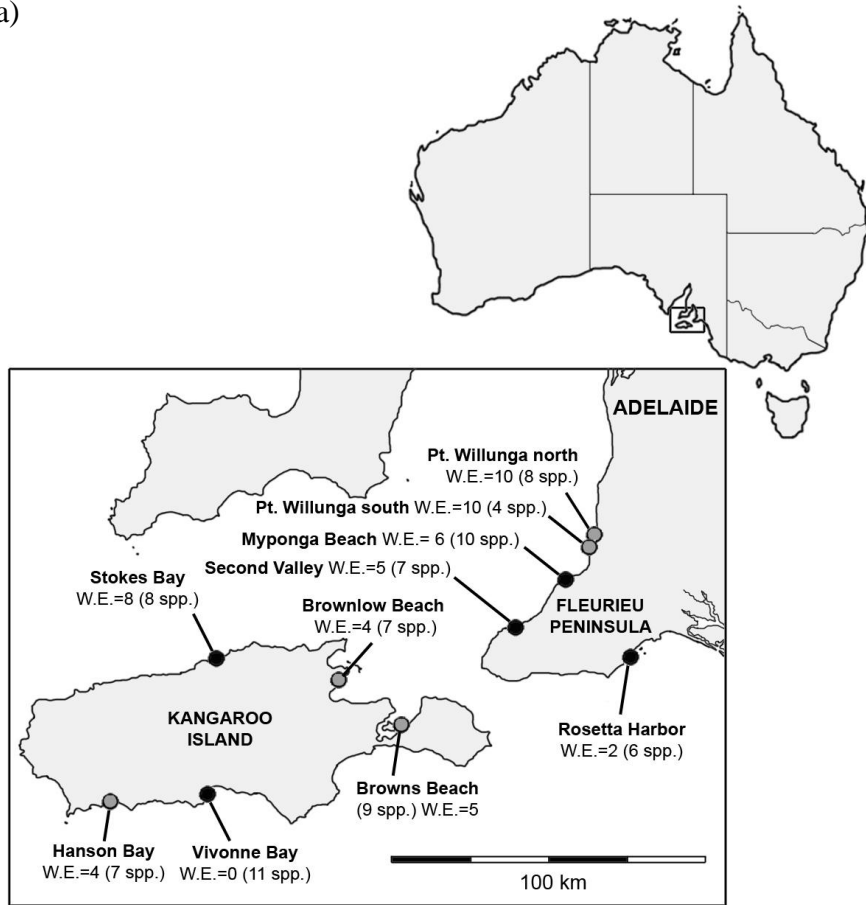
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75 **FIGURE 3:** Differences in mean (\pm S.E.) (a) abundance and (b) number of species of chitons
 76 found during one hour time search surveys in boulder-fields comprised of hard and soft rock
 77 types. Both measures were statistically similar among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

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

(a)



(b)



(c)



