Observations of relic intertidal assemblages in an inland marine-spring of Eyre Peninsula, South Australia

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Observations of relic intertidal assemblages in an inland marine-spring of Eyre Peninsula, South Australia

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ABSTRACT

Marine-springs containing relic intertidal species can be used to observe how assemblages usually found only on open coasts are structured when free from disturbances associated with water movement. This study tested if two previously described patterns from disturbance-prone boulder habitats occurred within a South Australian marine-spring. I aimed to determine how species are associated with the interface between boulders and the surface of the bottom sediment, a habitat feature suggested to be important for some key benthic invertebrates. Testing species associations to this feature is normally difficult because boulders and sediment are regularly disturbed, but on stable marine-spring boulders, fine-scale associations of species with this interface could be measured. Also investigated was a previously described negative correlation of peracaridan (Crustacea) densities with boulder size. This could possibly occur due to variability in disturbance related to boulder-size/stability, in which case the correlation would not be expected in this sheltered lake. Seven rocky-benthic marine species were found. The boulder–sediment interface could be easily located on overturned boulders. An anemone (*Isanemonia australis*) was highly abundant within 5 mm of this interface, providing evidence of this habitat feature's importance. As found previously, correlations were significant between boulder size and densities of peracaridans (in this case, the isopod *Zuzara venosa*). This correlation, which has been described widely for similar species, has previously been attributed to disturbance. This study found it occurring in extremely sheltered environments, however, so disturbance is unlikely to be involved. Additional larger-scale comparisons could provide further information about the effects of sheltered/exposed conditions on these taxa.

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Benthos; disturbance; saline lake; invertebrate; boulder habitat

Introduction

Marine-springs occur where groundwater from the sea diffuses through frontal dunes filling inland hollows (Timms, 2009). The lakes formed by these springs are sometimes populated by abundant marine species (Bayly, 1970; Halse et al., 2000; Timms, 2009). Microfauna can be introduced from the sea by birds (Bayly, 1970) while the presence of marine macrofauna is considered evidence that the lake was originally connected to the sea. This can occur when partially enclosed bays are dammed by transgressive dunes,

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with some marine species continuing to breed and maintain relic populations in the enclosed lake (Timms, 2009; Warren, 1982). Relics in such lakes can include pelagic fish, and benthic snails, bivalves, isopods and algae (Bayly, 1970; Halse et al., 2000; Timms, 2009; Timms, Coleman, & Cooper, 2014).

Marine-springs and habitats open to the sea can have many similar environmental conditions (e.g. salinity, water depth and variety of benthic substrata; Timms, 2009; Timms et al., 2014). One condition that differs largely, however, is the amount of disturbance related to water motion. In intertidal habitats open to the sea, disturbance to rocky and soft bottom habitats can be extreme (Grant, 1981; Shanks & Wright, 1986; Sousa, 1979). Even in habitats sheltered from waves, water motion from tidal movements shifts sediments and causes much physical dynamism (e.g. Alongi & Christoffersen, 1992). Areas where marine-springs occur are generally small (>1 ha in area; Timms, 2009), and the environmental forces causing physical disturbance of rock and sediment habitats are much less in such small water bodies (see, e.g., Hamilton & Mitchell, 1997) relative to most other shallow marine systems. Marine-springs, therefore, provide a unique opportunity to observe how intertidal species use these habitats without the disturbances that influence them in almost all other natural contexts. Because some species are common to both marine-springs and widely studied habitats open to the sea, information about species responses to extremes of habitat type can be gained from studying these sheltered water bodies.

This study took observations (Underwood, Chapman, & Connell, 2000) of ecological patterns in a marine-spring that forms part of "Seagull Lake" in western Eyre Peninsula, South Australia (latitude −32° 57′ 54″, longitude 134° 12′ 34″). The 0.12 ha spring has a near-constant salinity of 37–40 g/L and harbours 17 marine species (Timms et al., 2014). Several of these are benthic, attached to limestone boulders resting on the soft bottom of the lake bed. Disturbance from waves and water motion is generally considered one of the main processes structuring assemblages on unstable rocky substrata in shallow marine habitats (McGuinness, 1987a; Osman, 1977; Sousa, 1979). By investigating these substrata in Seagull Lake, it is possible to observe the patterns these same species form in an environment almost devoid of the ubiquitous physical disturbances occurring for unstable boulder habitats in environments open to the sea. Research from habitats with extremes of conditions such as marine-springs is useful because it provides information about the species-assemblage structure that will develop naturally, potentially over thousands of years (e.g. Timms et al., 2014), in habitats with unusual environmental conditions. These can be compared with assemblage structures in less extreme conditions, allowing inferences regarding effects of the relevant environmental factor. Also, the unusual conditions in habitats such as marine-springs may allow unique opportunities for observations that would not be possible in other habitats.

In shallow coastal boulder fields, the relationship between the size of a boulder and the frequency of its disturbance by water motion is negative (McGuinness, 1987a). Consequently, the disturbance that species on boulders are subject to often varies along the boulder size gradient (McGuinness, 1987b; Osman, 1977; Sousa, 1979). If, however, this effect of boulder size occurs in a disturbance-free environment, then disturbance can be ruled out as a cause of the effect. One aim of this study was to investigate if effects of boulder size were evident for benthic species in Seagull Lake, to determine if such relationships can be formed in the absence of the disturbances that are usually attributed as the cause (e.g. McGuinness, 1987b). If disturbance is important for producing effects of boulder size for these species, then I would hypothesise that no relationship between biotic structure and boulder size will occur in this sheltered lake. This test, therefore, provides information relevant to the influence of disturbance processes (e.g. Connell, 1978) not only in marine-springs but also in the wide range of other habitats where the marine-spring species occur.

The association of benthic fauna to the area around the interface between boulders and the sediment they rest on was also investigated. Previous research has suggested that this interface may be an important habitat feature for boulder species, especially when it occurs on the very surface of the sediment (Le Hir & Hily, 2005; Liversage, Cole, McQuaid, & Coleman, 2012), where it is represented as a line around the rim of the boulder. It is difficult, however, to determine exactly where the interface is positioned on boulders overturned for sampling in disturbance-prone environments. In addition, the position of this interface line can be expected to change frequently with movement of the boulder and the underlying substratum. Therefore, an accurate picture of how species use the interface is difficult to achieve. When boulders in Seagull Lake were overturned, however, it was possible to clearly see the line around the boulder where this interface was positioned. These boulders had remained stable for at least the length of time required for the limestone directly above the interface to be coloured green from microalgae and underneath the rock was either clean white or stained black from anoxic iron monosulphides (Rusch, Topken, Bottcher, & Hopner, 1998). In either case, the line of demarcation between the area above and below the sediment was clear. The second aim of this study was to determine if this interface specifically is a beneficial habitat feature for benthic species, in which case it would be predicted that faunal densities will be greater along the line of the interface than elsewhere on the boulder.

Methods

Invertebrates and algae were sampled on boulders in the marine-spring at Seagull Lake which ranged in surface area from 156 to 1122 cm^2 (approximately 10–40 cm in length). Three random sites in the spring were sampled, each having three boulders. Fine-scale sampling to measure how species use the area around the boulder/sediment interface was done from six quadrats on each of the nine randomly chosen boulders across the marine-spring. Sampling was done in April 2013 and repeated on different boulders in the same sites in January 2016, incorporating seasonal variability across autumn and summer. The marine-spring area is controlled mostly by marine influences with factors such as salinity remaining relatively constant throughout the year (Timms et al., 2014); however, factors such as water level do fluctuate seasonally, so different results may be found at other times/seasons.

Boulders were overturned and photographs that included scale bars were taken of the uppersides, undersides and edges. Care was taken to minimise disturbance as boulders were overturned, but the sampling likely resulted in some disturbance (Chapman & Underwood, 1996). Boulders were scarce in the marine-spring, and because a large proportion of all available boulders were overturned using this experimental design, sampling of greater numbers of boulders was not done. The surface around the edge of each boulder was divided into six even segments in the photographs, and each segment was randomly allocated to be sampled at one of two positions: (1) the position immediately above the interface of the boulder and the surface of the sediment, up to 5 mm and (2) the position above 5 mm from interface, up to the boulder's edge, defined as the line around the boulder half way between the centre of the upper and undersides (Figure 1). The distance of 5 mm was chosen because this is the approximate average body length of the invertebrates using the interface, so if the centre of an individual's body is within this distance, it is probably in contact with the interface. Species that used the interface were generally not found on positions other than the two sampled, so other positions were not included in this comparison. Counts were converted to densities to allow comparison between positions of differing area, then comparisons between the interface position and the position above the interface were done using ANOVA in GMAV5 (University of Sydney). Factors were Site (random), Boulder (random, nested in Site) and Area on boulder (fixed). Separate analyses were done for the two sampling times. Cochran's test was used to test the assumption of homogeneity of variances (Underwood, 1997).

Counts were also made across whole boulders to compare densities on boulders differing in size. Attempts were made to include large-scale comparisons with nearby boulder habitats open to the sea, but these habitats did not have sufficient abundances of the marine-spring taxa for analysis. Sampling was, therefore, limited in this study to the marine-spring, with information about exposed habitats for comparison taken only from previous studies, in which sufficient abundances of these taxa were found. Species densities were calculated by dividing counts by boulder surface areas. These were estimated by importing photographs of boulders, including a scale, into the programme SketchUp (http://www.sketchup.com/) and producing a three-dimensional model from which the surface area could be calculated by the programme. This allowed the surface-area estimates to incorporate the depressions and pits that sometimes occurred on the

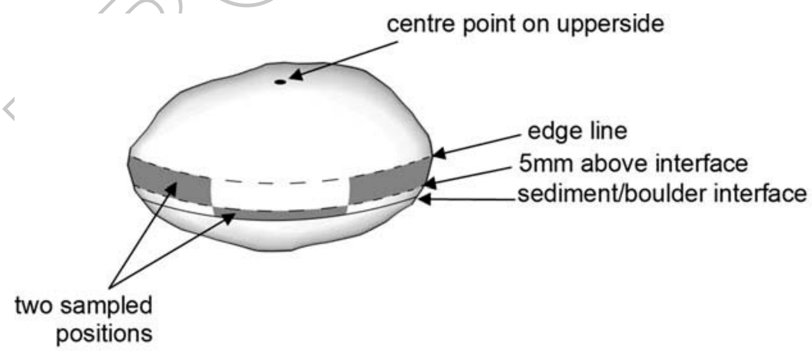

Figure 1. Representation of a hypothetical boulder, viewed from the side, showing the features used for defining where sampling was replicated across boulder surfaces. Six areas were sampled around the rim of each boulder; three are shown on the diagram shaded grey. Half the sampled areas were in the position within 5 mm of the interface between the boulder and sediment surface, and half above that position up to the boulder's edge line. This line was defined as the line around the boulder half way between the centre point of the upper- and undersides.

undersides of these boulders. Permutational ANCOVA using PRIMER v6 was done to test the correlation of species densities with boulder size, across boulders from the three sites at the two times. Boulder size was a continuous dependent variable while Time and Site were categorical random factors. The resemblances were calculated with the Euclidean distance measure and Type III sums of squares (Anderson, Gorley, & Clarke, 2008). The analysis used 9999 permutations. In cases where the covariate was associated significantly with the response variable, the relationship was assessed graphically on scatter plots with linear regression used to plot a trend line. In all analyses, if the *P*-values of interaction terms that included a random factor were >0.25, they were eliminated from the analysis to provide a more powerful test for the relevant null hypotheses (Underwood, 1997).

Results

Six macroinvertebrates and one macroalga were observed using the rocky substrata across three sites in Seagull Lake (Table 1). The isopod *Zuzara venosa* was the most abundant, but they moved across the boulder surface quickly when lifted and so associations with positions on boulders could not be measured. The second most abundant species was the anemone *Isanemonia australis*. Most individuals were found on or near the boulder/sediment interface (Figure 2). During the first sampling time, the mean density of *I. australis* in the area within 5 mm of the interface was consistently greater than in the area higher than 5 mm above the interface by a factor of approximately 7 (Table 2, Figure 3a). During the second sampling time, the factor Position on Boulder interacted with the random factors (Table 2) indicating spatial variability in patterns, likely caused by some of the boulders having few if any anemones in any quadrats. SNK tests indicated that on four of the seven boulders that had anemones, there were greater densities in quadrats within 5 mm of the interface, and in no instances were there greater densities on other areas of the boulders (Figure 3b).

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The three most common species were sufficiently abundant across the boulders to test if their densities were correlated with boulder size. *Z. venosa* densities were negatively correlated with boulder size and this was consistent among sites and times (Table 3, Figure 4). No effects of boulder size or of the random factors were found for *I. australis* and *Austrocochlea porcata* (Table 3).

Table 1. List of species found on rocky substrata in the marine-spring at Seagull Lake.

Phylum/ division	Class	Family	Species	Mean no. per boulder	Proportion of boulders it occurred on
Cnidaria	Anthozoa	Actiniidae	*Isanemonia australis*	14.61	1
Arthropoda	Malacostraca	Sphaeromatidae	*Zuzara venosa*	11.67	0.94
		Idoteidae	*Euidotea danai*	0.06	0.06
Mollusca	Gastropoda	Trochidae	*Austrocochlea porcata*	4.30	0.83
		Hydrococcidae	*Hydrococcus brazieri*	1.89	0.11
		Batillariidae	*Zeacumantus diemenensis*	0.89	0.11
Chlorophyta	Ulvophyceae	Polyphysaceae	*Acetabularia peniculus*	9,56	0.22

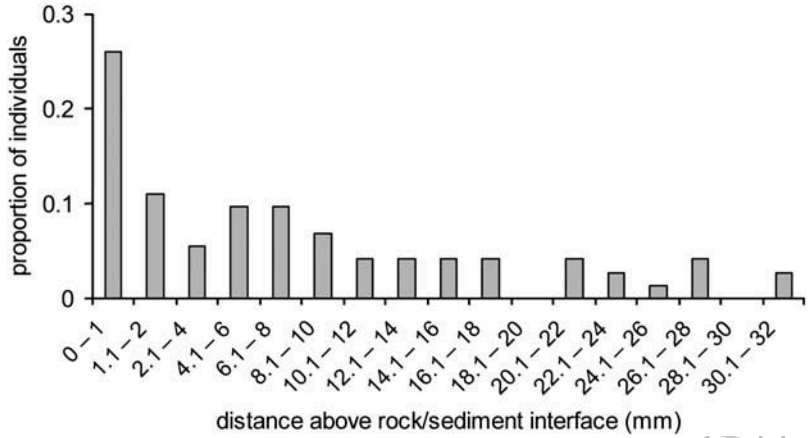

Figure 2. Frequency distribution of proportions of the total numbers of *Isanemonia australis* found at different distances above the rock/sediment interface on boulders resting in the sediment of the lake bed.

Table 2. ANOVA comparing densities of an anemone from quadrats positioned either within 5 mm of the boulder/sediment interface or from above the 5 mm line to the boulder's edge.

		Isanemonia australis					
		Time 1[a]			Time 2[b]		
Source	df	MS	*F*	*P*	MS	*F*	*P*
Site = Si	2	7.21	0.01	>0.75	2379.70	0.35	>0.5
AQ7 Boulder = Bo(Si)	6	485.94	0.49	>0.75	6797.76	5.95	**<0.001**
Position on boulder = Po	1	5344.08	5.34	**<0.05**	24915.15	5.03	>0.05
Si x Po	2	263.78	–		1510.61		–
Po x Bo(Si)	6	648.86	–		4948.51	4.33	**<0.01**
Residual	36	1000.18			1141.82		

There was three of each quadrat position per boulder, on three random boulders at each of three random sites. Sampling was repeated at two random times. The factors Site and Boulder (nested in Site) were random; Position on boulder was fixed. When *P*-values of interaction terms were >0.25, they were eliminated from the analysis to provide a more powerful test for the relevant null hypotheses (Underwood, 1997).
Eliminated term is denoted by "–".
[a]Cochran's test $C = 0.30$, $P > 0.05$.
[b]Cochran's test $C = 0.27$, $P > 0.05$.

Discussion

Some clear patterns of association of benthic species to certain microhabitat features were able to be discerned due to the disturbance-free nature of this marine-spring. Marine species including gastropods (Addessi, 1994), chitons (Liversage & Benkendorff, 2013) and algae (Choi & Ginsburg, 1983; Liversage, 2015a; Liversage & Kotta, 2015) are known to be associated with the edges or rims of boulders, suggesting that there is a feature or condition there that these species find beneficial. Here, the hypothesis was tested that the interface between the boulder and the surface of the sediment substratum is one important feature around boulder edges, and this hypothesis was accepted for the anemone species in Seagull Lake.

The reason for the importance of the interface may be related to a number of factors. For example, energy expenditure is required for animals such as anemones to maintain

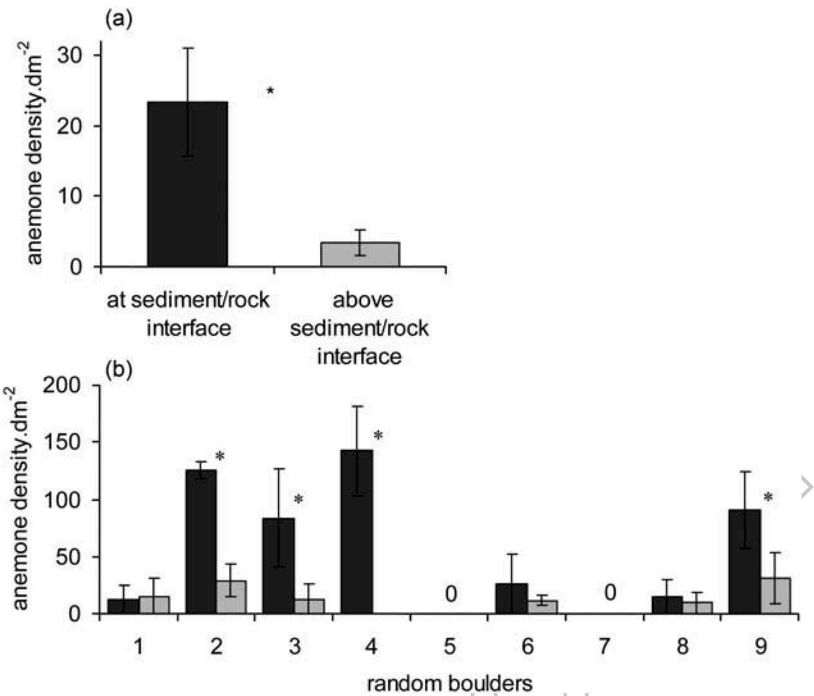

Figure 3. Mean (±SE) densities of the anemone *Isanemonia australis* at (a) Time 1 and (b) Time 2 that were located within 5 mm of the sediment/boulder interface (shaded dark grey), or above that position up to the boulder's edge (shaded light grey). Data from Time 1 are shown pooled from the nine random boulders; $n = 3$ quadrats. * Denotes that significant differences between treatments were found using SNK tests.

Table 3. PERMANOVA on the densities of an isopod, anemone and gastropod occurring in Seagull Lake.

	Zuzara venosa			*Isanemonia australis*			*Austrocochlea porcata*		
Source	df	MS	*F*	df	MS	*F*	df	MS	*F*
Boulder size = Bo	1	72.62	7.04*	1	0.004	0.001	1	0.05	0.10
Site = Si	2	36.83	3.57	2	8.341	1.453	2	1.17	2.47
Time = Ti	1	8.67	0.84	1	25.629	4.464	1	1.45	3.07
Bo x Si	2	31.00	3.01	2	–		2	–	
Bo x Ti	1	–		1	–		1	–	
Si x Ti	2	–		2	–		2	–	
Bo x Si x Ti	2	–		2	–		2	–	
Residual	11	10.31		13	5.74		13	0.47	

Comparisons were between three random sites and two random times, and had the surface area of boulders as a continuous variable; $n = 3$.
Eliminated term is denoted by "–".
*$P < 0.05$.

attached to a hard substratum by muscular or chemical means (Young, Yule, & Walker, 1988). It is possible that when an anemone is surrounded by sediment at the interface with a hard substratum, the sediment provides physical support, reducing energy expenditure. Alternatively, the interface may be important for reasons related to predation. 205 Seagull Lake contains predators (Timms, 2009) and anemones may be more

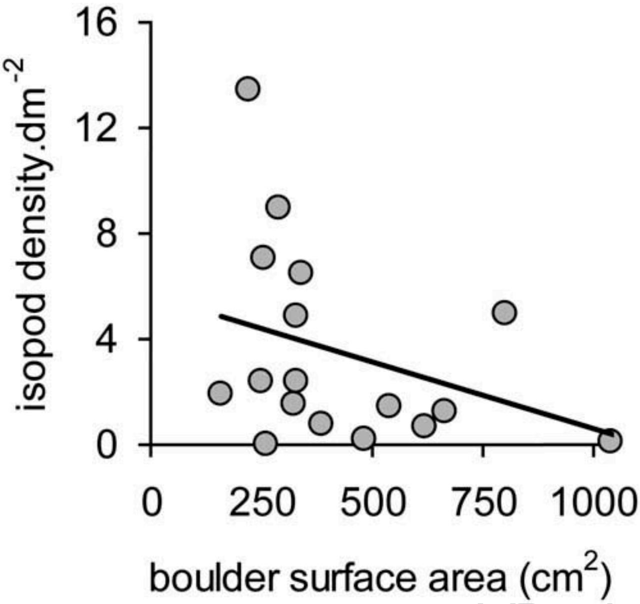

Figure 4. Correlation between density and boulder size for the isopod *Zuzara venosa*. Linear regression was used to visually represent the result from the ANCOVA. Data were pooled from three random sites sampled at two random times; n = 3 boulders.

sheltered from predatory fish (Ates, 1989) or molluscs (Perron & Turner, 1978) when occurring at this interface. Another possibility is that the topography of the benthos is affecting water flow and increasing deposition of particulate matter around features such as boulders (Bouckaert & Davis, 1998), which these anemones at the boulder/sediment interface may be responding to. Similar processes may be occurring for this anemone, and other benthic species, in marine habitats open to the sea. Determining this in a physically dynamic environment where rocks and sediment are being regularly shifted, however, would be difficult, and may explain why evidence of this association does not appear to have previously been described.

For *I. australis* and *A. porcata*, there was no evidence that densities varied according to the size of the boulders. Many sessile species are affected by the size of boulders due to the differing amounts they are subject to physical disturbance (McGuinness, 1987b; Osman, 1977; Sousa, 1979). The size of boulders also affects habitat suitability for some mobile species (Liversage, 2015b; McClintock, Angus, & McClintock, 2007), likely due to disturbance dynamics (e.g. Chapman & Underwood, 1996; Smith & Otway, 1997). For *I. australis* and *A. porcata*, when living free from typical shallow marine disturbances, they do not associate with boulders of certain sizes as may be expected in a high-energy environment. Further, direct comparisons of how these species associate with different sized boulders in high- and low-energy environments would be useful.

The negative correlation found between boulder size and density of *Z. venosa* is similar to the correlation that peracaridans have displayed in previous studies (Grzelak & Kuklinski, 2010; Liversage & Kotta, 2015). Peracaridans often have important roles in benthic communities (Cronin & Hay, 1996; Duffy & Hay, 2000; Engkvist, Malm, & Tobiasson, 2000), so it is important for our understanding of their ecology to test if this widespread population pattern is related to disturbance. It was found presently that this correlation can occur in an environment free from typical shallow marine disturbances. It is, thus, likely that the correlation is not due to any dynamic involving disturbance. Structural aspects of the boulders themselves may be involved, but it is not obvious what aspects of small boulders may be beneficial to peracaridans such as amphipods and isopods. It is possible that larger boulders have a greater proportion of their surfaces inserted more deeply into the underlying substratum, and these surfaces cannot be readily colonised. Larger boulders also have a lower proportion of edge habitat relative to small boulders, and some benthic invertebrates find edge habitat beneficial, as was found for *I. australis* in this study and species such as chitons in previous studies (Liversage et al., 2012). These possibilities should be focused on in further research building on from these observations. These results can be considered preliminary as only a small number of boulders naturally occur in the spring, so the sample size of the present study was limited by this. Further research should consider addition of new boulder habitat (e.g. Chapman, 2011; Liversage, Janetzki, & Benkendorff, 2014; although any manipulations of the spring should be done with caution given the rarity of marine-springs and their vulnerability to disturbance; Timms, 2009). Such research should also ideally incorporate additional marine-springs. While this study did assess spatial variation within the Seagull Lake spring, assessment of more than one marine-spring would be necessary to provide information about variation across larger spatial scales.

In conclusion, by taking observations in this marine-spring free from the disturbances typical of intertidal habitats, it was found that the interface between rock and sediment is an important habitat feature for a common Australian anemone, and that disturbance is unlikely the cause of the widely observed association of peracaridan crustaceans to small boulders. Similar dynamics may also apply to other species that use marine boulder habitat, some of which are ecologically (e.g. Smoothey & Chapman, 2007) or commercially (e.g. McCormick, Herbinson, Mill, & Altick, 1994) important. Marine-springs provide a useful tool for understanding processes structuring communities by allowing observations in natural conditions very different to almost all other shallow marine environments. Further information could be gained by taking larger-scale observations or performing manipulative experimentation in this unique environment.

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Disclosure statement

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