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Spatial variation in burrow morphology of the mud shore crab *Helograpsus haswellianus* (Brachyura, Grapsidae) in South Australian saltmarshes

G. Katrak[A,C], *S. Dittmann*[A] *and L. Seuront*[A,B]

[A]School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia.
[B]South Australian Research and Development Institute, Aquatic Sciences,
West Beach, SA 5022, Australia.
[C]Corresponding author. Email: gitanjali.katrak@flinders.edu.au

Abstract. Burrowing by crabs is an important component of their functional role in mangrove and saltmarsh habitats. The grapsid crab *Helograpsus haswellianus* (Whitelegge, 1889) is one of the more conspicuous burrowing organisms in the saltmarshes of southern Australia. To evaluate intraspecific differences in burrowing behaviour among saltmarshes on a regional scale, we compared vegetation cover, sediment composition and burrow morphology at four sites using resin casts. Six burrow morphology characters were measured (burrow depth, number, lengths and diameter of the shafts, ratio of the shafts, number and diameter of the burrow openings), and the overall 3D burrow complexity was described using a single parameter, the fractal dimension *D*. Apart from the number of shafts, all morphological characters of the burrows differed significantly among sites. Analyses of the fractal dimensions lead to the identification of three groups of burrows based on *D*: a group of highly complex burrows (one site), a group of burrows of intermediate complexity (two sites) and a group of less complex burrows (one site). Burrow morphology variation was correlated with non-dominant vegetation, plant matter in the soil and very coarse sand in the sediment. Site-specific differences in burrows caution against generalising the functional role of crabs across sites.

Additional keywords: burrows, crab, ecosystem engineer, fractals, resin cast, saltmarsh.

Introduction

Burrowing is a widespread behaviour among invertebrates in marine soft sediments. The resulting biogenic structures and the engineering processes involved in constructing and maintaining them generate complex interactions that co-exist alongside trophic webs (Reise 2002; Kristensen 2008). The effect of an organism on the surrounding sediments is dependent on the type of burrow constructed. For example, burrow lining can affect sediment rigidity and the diffusion rates of porewater (Jones and Jago 1993; Hannides *et al*. 2005). Burrow depth, morphology and the irrigation intensity by the burrow-dweller further affect sediment properties and biogeochemistry (Mermillod-Blondin *et al*. 2004; Kristensen 2008).

The morphology of burrows is mostly species-specific (Griffis and Suchanek 1991; Wolfrath 1992). However, given the wide variety of physical and chemical factors between different sediment types and vegetation, burrowing species might modify burrow architecture to adjust to a specific suite of environmental parameters (Griffis and Chavez 1988). Crabs are among the larger, more conspicuous burrowers and some species have significant intraspecific variation in their burrow morphology in relation to environmental factors, such as sediment composition, substratum hardness and root-mat density of the surrounding vegetation (Bertness and Miller 1984; Takeda and Kurihara 1987; Morrisey *et al*. 1999). Burrow morphology can also vary with shore height and tidal period, as well as with the sex and age of the crabs (Lee and Koh 1994; Lim and Diong 2003; Chan *et al*. 2006).

Burrows are important for protection from desiccation for crabs such as *Helograpsus haswellianus* (Whitelegge, 1889) and are regularly maintained (Higgenbottom 1982). *Helograpsus haswellianus* (Grapsidae) is endemic to Australia, where it is widespread around the southern and eastern coasts (Hale 1927; Griffin 1971; Marsh 1982; Breitfuss 2003). It occurs in a wide range of habitats from mangrove areas that are inundated daily to the supralittoral fringes of saltmarshes that are inundated only by spring tides (McKillup and Butler 1979; Marsh 1982; Breitfuss 2003). We hypothesised that the morphology of the burrows would vary among sites with different vegetation and sediment composition. More specific hypotheses included: (1) burrows would be more complex in areas with denser vegetation/root matter because of a need to burrow around the obstructions; and (2) burrows would be more complex in muddier sediments because of the more cohesive nature of the sediments. Such variation in burrow morphology could result in differing ecological roles of *H. haswellianus* in different types of habitats, which has been addressed in further studies. In the present study, we investigate the structural complexity of *H. haswellianus* burrows in

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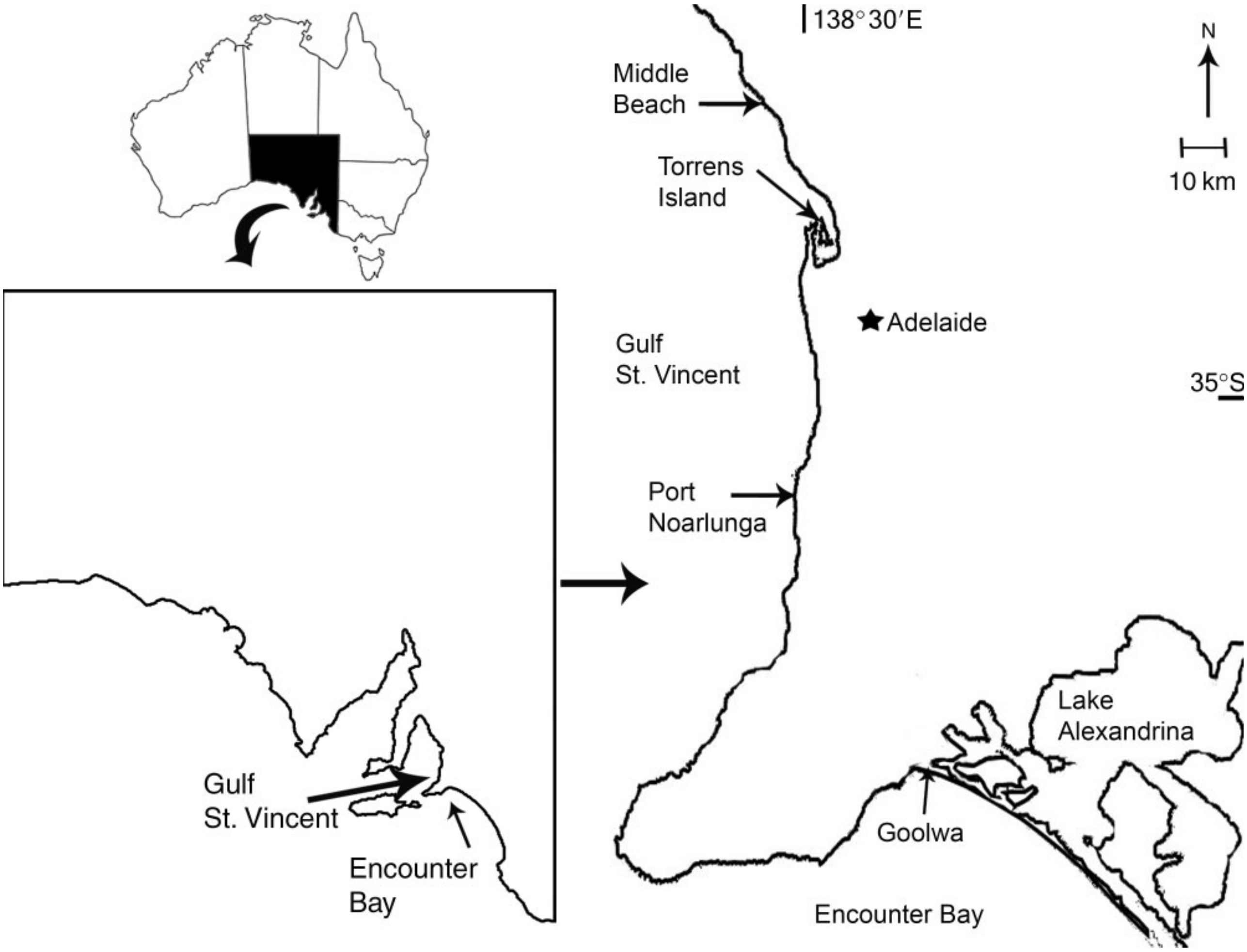

Fig. 1. Location of the field sites along the coastline of South Australia.

different saltmarshes in South Australia and assess how sediment composition and vegetation influence the burrow morphology of this species.

The standard method to assess burrow morphology consists of measuring a series of parameters from resin, wax or plaster of Paris casts, such as burrow depth, number, length and diameter of the shafts, and the number and diameter of the burrow openings (Lim and Diong 2003; Thongtham and Kristensen 2003; Rudnick *et al*. 2005; Chan *et al*. 2006). However, because the interactions between these traditional parameters are unclear (Romanach and Le Comber 2004), we also used fractal geometry, which has the desirable property of using a single measure, the fractal dimension *D*, to quantify the geometric complexity of burrows. This method has been successfully applied to describe the complexity of a range of subterranean rodent habitats (e.g. Le Comber *et al*. 2002, 2006; Sumbera *et al*. 2003; Romanach 2005). To the best of our knowledge, fractal geometry has never been used on crab burrow morphology.

Materials and methods

Study sites

Four temperate saltmarshes were sampled in South Australia from December 2005 to January 2006. Three of the sites, Middle Beach (34°36′S, 138°24′E), Torrens Island (34°48′S, 138°32′E) and Port Noarlunga (35°9′S, 138°29′E), are along the Gulf St Vincent and the fourth site, Goolwa (35°32′S, 138°50′E), is situated in Encounter Bay (Fig. 1). Gulf St Vincent has an ~2.5 m spring tide range, whereas Encounter Bay is microtidal (maximum tidal height <1.5 m). Thus, Middle Beach is inundated daily, whereas the saltmarsh at Goolwa is only submerged by the highest spring tides. Sampling sites at Torrens Island and Port Noarlunga were inundated by spring tides, but not always covered by neap tides. Water level above the sediment during spring tides in the experimental areas was 0–20 cm at Goolwa, 0–50 cm at Port Noarlunga, 10–70 cm at Torrens Island and 50–>90 cm at Middle Beach. The sites were chosen because in addition to the differences in exposure, the sites differed markedly with regard to the type of vegetation present (Table 1).

Field surveys, sediment analyses and cast measurements

An experimental area where crabs had been found, encompassing all of the low marsh vegetation observed at the site, was chosen within each site. Burrow counts were conducted to determine if burrow-opening density would give some indication of the number of burrows present beneath the surface. Burrow-opening

Table 1. Vegetation type and density and number of burrow openings within the resin casting areas (0.06 m^2) at various sites
DV, dominant vegetation; NDV, non-dominant vegetation; %ovc, % overhanging vegetation cover; %fss, % free soil on surface

Site	Vegetation present at site	Quadrat	No. openings	DV within the quadrat	NDV within the quadrat	%ovc	%fss
Goolwa	*Sarcocornia quinqueflora*, *Suaeda australis*, *Samolus repens*, *Halosarcia* sp., *Frankenia pauciflora*	1	3	*S. quinqueflora*	*S. australis*	100	70–75
Port Noarlunga	*Sarcocornia quinqueflora*, *Suaeda australis*, *Sclerostegia arbuscula*	1	7	*S. quinqueflora*	*S. australis*	20–30	90–95
		2	9	*S. australis*	*S. quinqueflora* *S. arbuscla*	20–30	85–90
Torrens Island	*Avicennia marina*, *Sarcocornia quinqueflora*, *Suaeda australis*, *Sclerostegia arbuscula*, *Samolus repens*, *Halosarcia* sp.	1	6	*S. quinqueflora*	*S. quinqueflora* *Halosarcia* sp.	85–90	65–70
		2	4	*S. quinqueflora*	*S. arbuscla* *A. marina*	85–90	50–55
Middle Beach	*Avicennia marina*, *Sarcocornia quinqueflora*	1	4	*S. quinqueflora*	–	85–90	95–99
		2	12	Bare mud	–	0	100

density within the experimental area was estimated by randomly placing a 0.25-m^2 quadrat (eight replicates) and counting the number of burrow openings within the quadrat.

For the resin casting, two 0.06-m^2 quadrats were haphazardly arranged within the experimental area and the type of vegetation, % vegetation cover, % free soil on the surface and the number of openings within the quadrat were noted (Table 1). The dominant vegetation was defined as the plant species that constituted more than 50% of the total vegetation present within the quadrat. The plant species present were classified as non-dominant vegetation when they constituted less than 50% of the total vegetation within the quadrat. Percentage cover consisted of the percentage of the total surface area of the quadrat that was shaded or covered by plant matter growing within the quadrat as well as overhanging branches of plants outside the quadrat. Percentage free soil was defined as the percentage of the total surface soil within the surface area of the quadrat that did not have roots/stems penetrating the surface.

A liquid epoxy resin (3 : 1 Araldite to hardener; Adelaide Epoxy Supplies, Adelaide, South Australia) was poured into all burrow openings within the 0.06-m^2 quadrat and left to harden for ~48 h. The casts were then dug up and cleaned to remove as much sediment as possible from the surface. There was no upwelling of water when the casts were excavated, indicating that the burrows had not touched the watertable. As only complete casts were used for analysis, casts were obtained from only one quadrat at Goolwa. A total of 36 complete casts (13 from Middle Beach, seven from Torrens Island, 14 from Port Noarlunga and two from Goolwa) were obtained from all sites. Given the size of the burrow casts found at Goolwa and the destructive nature of resin casting, it would do a greater amount of damage to the saltmarsh to obtain more casts from this site to equal numbers obtained at the other sites.

After the casts were excavated, two sediment cores (up to 30 cm sediment depth) were taken adjacent to the casting area for each quadrat. These cores were divided into six 5-cm horizons to analyse vertical differences in sediment composition. Samples were wet sieved through a 1-mm sieve and the sediment retained on the sieve was dried and weighed. When plant matter (e.g. root fibres) was present, the retained sample and the plant matter were measured separately and the percentage of plant matter present in the sample was calculated. The grain size composition of the sediment was analysed using a laser diffraction particle size analyser (Hydro2000MU; Malvern Instuments, Worcestershire, UK).

The burrow depth, number of shafts, length of burrow shafts, diameter of burrow shafts, number of burrow openings and diameter of burrow openings were recorded for each cast. The depth was measured as the straight distance between the surface and the deepest point of the cast, whereas the length was measured as the curved distance between the burrow opening to the end point of the burrow shaft. For burrow shafts with multiple openings, an average of the lengths was used. As the shape of the burrow openings was irregular, four separate measurements were taken for each opening and the mean value was used. The average diameter of the shaft was calculated from measurements taken every 5 cm along the shaft using a calliper.

Data analysis

We investigated the 3D complexity of the crab burrows by the box-counting method, an analysis that has been previously applied to other branched structures, such as terrestrial and marine vegetation (Morse *et al.* 1985; Abraham 2001). Each individual burrow cast was photographed twice, each photo being at right angles to the other. These orthogonal photographs were used to measure the 2D D value of each cast. The fractal dimension, D, was estimated by superimposing a regular grid of squares of size l on the object and counting the number of 'occupied' squares. This procedure was repeated using different values for l. The surface occupied by a burrow is then estimated with a series of counting squares spanning a range of surfaces down to some small fraction of the entire surface. The number of occupied squares increases with decreasing square size, leading to the following power-law relationship:

$$N(l) \propto l^{-D}, \tag{1}$$

where l is the box size, $N(l)$ is the number of squares occupied by the burrow and D is the box-counting fractal dimension, often referred to as the box dimension. D is estimated from the slope of the linear trend of the log–log plot of $N(l)$ *v.* l. Because slight reorientation of the overlying grid can produce different values of $N(l)$, D has been estimated for rotation of the initial 2D grid of 5° increments from 0 to 45° (Seuront *et al.* 2004). The 3D complexity for each cast was subsequently estimated as $D = (D_1 + D_2)/2$, where D_1 and D_2 are the fractal dimensions of two orthogonal views of the corresponding burrow (e.g. Seuront *et al.* 2004).

Statistical analyses were carried out with SPSS version 14 and PRIMER v5. Burrow-opening counts met assumptions of normality (Kolmogorov–Smirnov test) and homogeneity of variances (Levene's test) and were analysed using a one-way ANOVA. Post-hoc analysis was carried out using Tukey's honestly significant difference (HSD) test. Non-parametric tests were used for the cast characteristics because they did not meet assumptions of normality even after square-root and $\log_{10}$ transformations. The fractal dimensions D_1 and D_2 for each cast were compared using a modification of the Student's t-test (Zar 1999). Differences in fractal dimensions among sites were inferred using the Kruskal–Wallis H-test, and a multiple comparison procedure (the Nemenyi Q test) was subsequently used to identify distinct groups of measurements.

Multi-dimensional scaling (MDS) was carried out to find patterns in burrow assemblages and environmental factors. Burrow characteristics were correlated with environmental variables using the BIOENV procedure of PRIMER. This test identified the environmental variables that best explained the variation in burrow morphology. BIOENV is a non-parametric method that calculates Spearman rank correlation coefficients (ρ) between the abiotic similarity matrix (burrow characters) based on the Bray–Curtis similarity index and the matrix of potential explanatory variables (environmental variables). Separate BIOENV tests were run for the sediment composition of the entire core and for the separate sediment horizons.

Results

Burrow-opening, vegetation and sediment features

The density of burrow openings within the experimental areas varied significantly among sites (ANOVA, d.f. = 3, $F = 19.07$, $P < 0.001$) and was highest in the sparse saltmarsh at Middle Beach (number of burrow openings per 0.25 m was 25.63 ± 2.80; mean ± s.e.) and lowest in the dense saltmarsh at Torrens Island (4.63 ± 1.58). The densities of burrow openings at the other two sites were between these values (13.50 ± 2.17 at Port Noarlunga and 10.13 ± 1.23 at Goolwa).

The density of burrow openings at Middle Beach was significantly different from that at each of the other three sites (Tukey's HSD $P < 0.001$ for the comparisons with Torrens Island and Goolwa and $P = 0.001$ for the comparison with Port Noarlunga). The burrow-opening density at Port Noarlunga also differed significantly from that at Torrens Island (Tukey's HSD $P = 0.02$). There were no significant differences in burrow-opening density between Port Noarlunga and Goolwa or between Torrens Island and Goolwa.

The type and density of vegetation within the casting area differed among sites (Table 1). *Sarcocornia quinqueflora* (Ungern Sternberg, 1866) was the dominant vegetation within most of the quadrats. *Suaeda australis* (Robert Brown, 1810) was dominant within one of the quadrats at Port Noarlunga, whereas one of the quadrats at Middle Beach was on a bare mud patch. The mangrove *Avicennia marina* (Pehr Forsskäl, 1775), which was present within one of the quadrats at Torrens Island, consisted only of pneumatophores.

Grain size analyses showed variation in sediment composition with depth and among sites (Table 2). Goolwa possessed fine sand sediments throughout, whereas the sediments at the other sites were composed of silt and mud near the surface and became sandier in the deeper layers. Fine fibrous root matter was found in various concentrations at all depths at Goolwa, Port Noarlunga and Torrens Island and up to a depth of 15 cm at Middle Beach. Unidentified, bulbous plant matter found in the sediments during cast excavation at Goolwa was not present in the cores.

Cast characteristics

The burrow casts showed a variety of morphologies, ranging from relatively simple, straight tubes with a single entrance to complex interconnected burrow shafts with multiple entrances (Fig. 2). Burrow depth, length of burrow shafts, diameter of burrow shafts, length/depth ratio, number of burrow openings and diameter of burrow openings varied significantly among sites (H-test, $P = 0.03$ for length/depth ratio, $P = 0.01$ for number of burrow openings, other characteristics $P < 0.001$; Table 3), whereas no significant difference was found for the number of main shafts ($P > 0.05$).

The burrows at Middle Beach were the shallowest (~10 cm) with the shortest shafts and narrow burrow openings (Fig. 2; Table 3). Burrow shafts at Port Noarlunga were straight compared with the more winding shafts observed at the other sites, and usually consisted of a single entrance, whereas those at Torrens Island had a higher number of openings per burrow and wider burrow openings than those at Port Noarlunga and Middle Beach respectively (Table 3).

Fractal analyses showed that all burrows investigated exhibited very strong scaling behaviour with coefficients of determination r^2 ranging from 0.96 to 0.99 over the whole range of available scales, that is, between 0.5 and 15 cm and between 0.5 and 50 cm for the smallest and largest burrows, respectively. The fractal dimensions, D_1 and D_2, estimated for each cast were never significantly different (t-test, $P > 0.05$) for the burrows investigated at Goolwa and Port Noarlunga, and only one and two burrows exhibited significant differences between D_1 and D_2 at Torrens Island and Middle Beach respectively. The resulting mean dimensional fractal dimensions D ranged between 1.61 and 1.64 at Goolwa ($D = 1.62 \pm 0.01$; mean ± s.e.), between 1.41 and 1.53 at Port Noarlunga ($D = 1.49 \pm 0.01$), between 1.50 and 1.59 at Torrens Island ($D = 1.55 \pm 0.01$) and between 1.50 and 1.65 at Middle Beach ($D = 1.56 \pm 0.01$) (Fig. 3). Significant differences were found between the fractal dimensions obtained from the burrow resin casts sampled at Goolwa, Middle Beach, Port Noarlunga and Torrens Island (Kruskal–Wallis test, d.f. = 3, $H = 19.75$, $P < 0.001$). More specifically, the fractal dimensions estimated at Middle Beach and Torrens Island

Table 2. Sediment characteristics at various depths next to the resin casts

Data are the range of values across the cores taken from each site. Plant matter and grain size fractions are expressed as the percentage found in the analysed sample. Only relevant grain size fractions found are listed

Site	Depth (cm)					
Grain size (mm)	0–5	5–10	10–15	15–20	20–25	25–30
Goolwa						
>1	0.07–0.66	0.00–0.04	0.00	0.00	0.00	0.00
0.125–0.25	31.85–36.54	32.89–36.70	35.25–35.68	44.90–46.78	33.31–40.93	49.86–50.06
<0.063	25.29–30.97	23.83–32.76	27.73–29.47	10.21–13.08	14.58–33.91	8.89–12.37
Median (mm)	0.13–0.15	0.14–0.16	0.15–0.16	0.19–0.21	0.14–0.20	0.18–0.19
Plant matter	1.97–3.23	0.59–1.00	0.20–0.89	0.24–0.41	0.22–0.26	0.39–0.72
Port Noarlunga						
>1	0.00	0.00	0.00	0.00	0.00	0.00
0.25–0.5	8.55–19.13	4.69–24.89	16.22–23.42	10.87–29.63	21.57–47.11	25.76–46.19
0.125–0.25	7.54–11.14	6.64–10.62	10.67–11.61	7.76–16.47	12.86–18.85	15.53–22.21
<0.063	56.26–75.66	45.60–77.38	48.52–61.78	39.65–72.51	18.39–50.18	15.31–39.30
Median (mm)	0.02–0.04	0.02–0.09	0.03–0.07	0.03–0.18	0.06–0.20	0.14–0.29
Plant matter	0.07–2.11	0.03–0.68	0.00–0.52	0.00–0.12	0.03–0.28	0.00–1.11
Torrens Island						
>1	0.00–0.22	0.00–0.33	0.00–0.11	0.00–0.06	0.00–0.22	0.00–1.49
0.125–0.25	12.54–18.69	3.63–20.00	4.92–15.55	7.12–43.37	14.68–48.64	17.77–43.24
<0.063	57.46–65.45	55.67–79.71	47.99–80.35	20.4–76.89	8.76–57.1	3.19–43.4
Median (mm)	0.03–0.05	0.03–0.05	0.01–0.07	0.02–0.14	0.04–0.18	0.08–0.20
Plant matter	1.96–9.79	1.29–6.09	0.23–6.32	0.10–0.76	0.00–3.30	0.00–13.58
Middle Beach						
>1	0.20–3.36	0.14–0.92	2.92–4.11	1.11–3.08	2.42–14.56	4.69–17.05
0.125–0.25	6.65–21.65	10.82–25.51	19.04–28.18	28.04–36.97	24.37–27.67	20.40–32.98
<0.063	40.86–72.99	32.53–63.18	23.57–40.34	9.56–22.18	8.84–19.68	7.71–9.07
Median (mm)	0.03–0.09	0.04–0.11	0.09–0.13	0.14–0.20	0.15–0.27	0.19–0.34
Plant matter	0.00–1.98	0.00–1.82	0.00–0.51	0.00–0.00	0.00–0.00	0.00–0.00

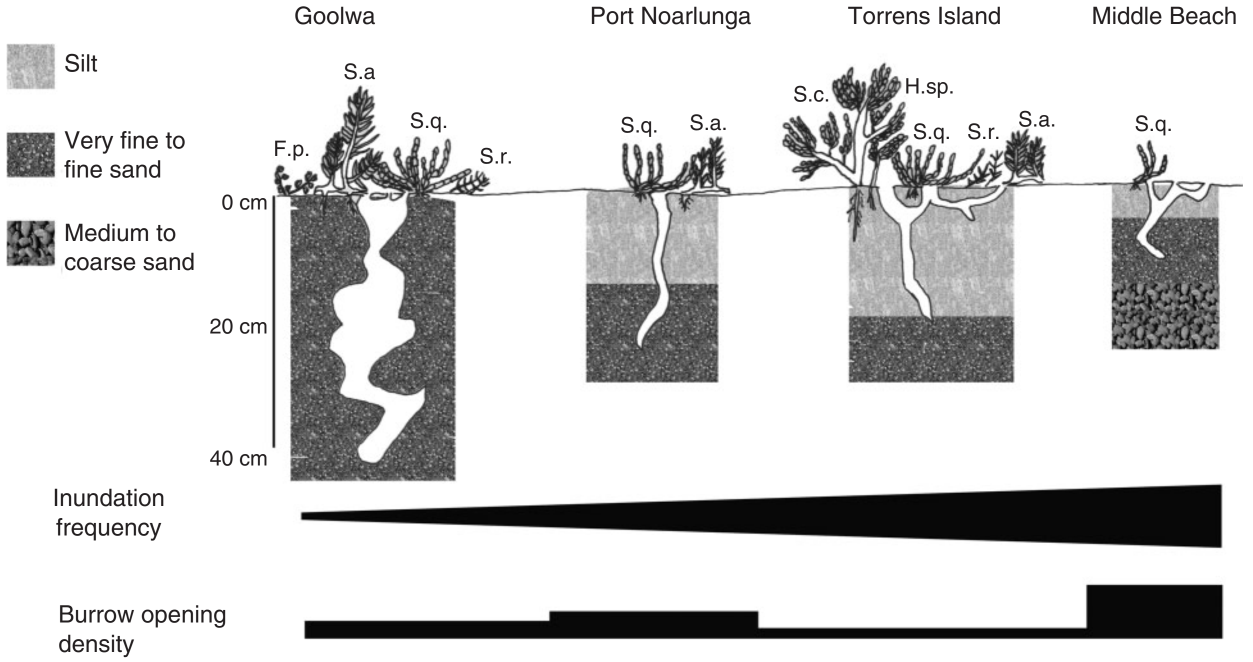

Fig. 2. Conceptual diagram of the variation in burrow morphology, vegetation type, vegetation density, sediment composition, inundation frequency and crab population density at the various study sites. Burrow complexity is based on the fractal dimension, *D*. S.q., *Sarcocornia quinqueflora*; S.a., *Suaeda australis*; S.r., *Samolus repens*; S.c., *Sclerostegia arbuscula*; F.p., *Frankenia pauciflora*; H.sp., *Halosarcia* sp.

Table 3. Morphological characteristics of *Helograpsus haswellianus* burrows based on resin cast measurements

Mean values ± s.e. are provided. H and P-values are the results from Kruskal–Wallis H-test (d.f. = 3 in all cases). ns, non-significant. Only comparisons with significant results in the Nemenyi test are provided (Critical values of Q at 0.05, 0.01 and 0.001 levels of significance are 2.64, 3.14 and 3.77 respectively). Ga, Goolwa; PN, Port Noarlunga; TI, Torrens Island; MB, Middle Beach

Variable	Goolwa	Port Noarlunga	Torrens Island	Middle Beach	H	P	Q tests
No. burrows	2	14	7	8	–	–	–
Depth of burrow (cm)	37.4 ± 0.3	25.5 ± 2.3	20.1 ± 2.1	10.6 ± 1.1	25.8	<0.001	MB & TI: Q = 2.66, $P < 0.05$ MB & PN: Q = 4.26, $P < 0.001$ MB & Ga: Q = 3.73, $P < 0.01$
No. main shafts	1.5 ± 0.5	1.0 ± 0.0	1.3 ± 0.2	1.2 ± 0.1	5.57	ns	–
Length of shaft (cm)	52.9 ± 4.6	28.0 ± 2.3	26.8 ± 2.7	13.5 ± 1.3	26.39	<0.001	MB & TI: Q = 3.24, $P < 0.01$ MB & PN: Q = 3.90, $P < 0.001$ MB & Ga: Q = 4.06, $P < 0.001$
Length/depth ratio	1.42 ± 0.14	1.11 ± 0.02	1.41 ± 0.17	1.31 ± 0.07	9.22	0.03	ns
Diameter of shaft (cm)	2.6 ± 0.1	1.4 ± 0.1	1.9 ± 0.1	1.2 ± 0.1	19.59	<0.001	MB & TI: Q = 3.27, $P < 0.01$ MB & Ga: Q = 3.46, $P < 0.01$ PN & Ga: Q = 2.89, $P < 0.05$
No. burrow openings	1.5 ± 0.5	1.2 ± 0.1	2.6 ± 0.4	1.5 ± 0.2	11.30	0.01	PN & TI: Q = 3.33, $P < 0.01$
Diameter of openings (cm)	2.0 ± 0.1	1.7 ± 0.2	2.4 ± 0.2	1.2 ± 0.1	20.57	<0.001	MB & TI: Q = 4.30, $P < 0.001$

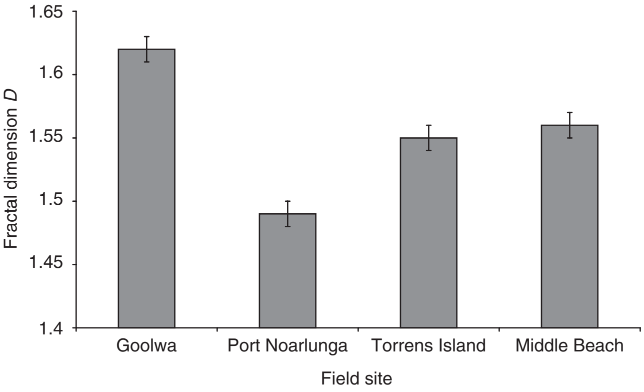

Fig. 3. Mean fractal dimensions (D) of burrow architecture at Goolwa, Port Noarlunga, Torrens Island and Middle Beach. Error bars represent s.e.

were not significantly different (Q test, $P > 0.05$), but significantly lower and higher (Q test, $P < 0.05$) than those estimated at Goolwa and Port Noarlunga respectively. This leads to the identification of three groups of burrow morphologies based on the fractal dimension D (Fig. 3). Therefore, burrows of decreasing complexity were observed at: (1) Goolwa; (2) Middle Beach and Torrens Island; and (3) Port Noarlunga.

Burrow complexity and environmental conditions

Based on the cast characteristics and fractal dimension D, MDS showed a greater similarity in the burrows at Torrens Island and Port Noarlunga, whereas burrows from Middle Beach and Goolwa were distinctly different (Fig. 4*a*). The best result for the BIOENV test comparing the similarity matrix of burrow characteristics to the environmental variables found a correlation ($\rho = 0.76$) between the burrows and the combination of non-dominant vegetation, the percentage of plant matter in the soil and the percentage of very coarse sand (Fig. 4*b*). Other combinations of environmental variables also produced good fits and always had at least one of the three mentioned variables present in them (Table 4).

The best fit in the BIOENV test comparing the burrow characteristics to the environmental variables by sediment depth found a correlation ($\rho = 0.83$) between the burrows and the combination of non-dominant vegetation and the percentage of very coarse sand at a depth of 10–15 cm (Fig. 4*c*). Other combinations that produced good fits consisted of combinations of the non-dominant vegetation and the percentage of very coarse sand present at depths greater than 10 cm (Table 4).

Discussion

The morphology of *Helograpsus haswellianus* burrows examined in the present study showed considerable variation in shape, size and complexity, ranging from single entrance shafts with no branches to interconnected shafts with multiple entrances. The surrounding vegetation and general sediment characteristics were found to be important factors influencing the morphology of the burrow for this species.

Burrow structure

As burrows are important as a refuge from desiccation for intertidal crabs (Takeda and Kurihara 1987; Thongtham and Kristensen 2003), the depth of burrows will be influenced by the water content of the sediment. Deeper burrows might also be a way of maintaining lower burrow temperatures in areas that are exposed for greater periods of time (Powers and Cole 1976; Wolfrath 1992; Lim and Diong 2003). We found the deepest burrows at Goolwa, where the saltmarsh is inundated only by the highest spring tides, whereas the shallowest burrows were at Middle Beach, which is inundated daily. Burrows from Port Noarlunga and Torrens Island were of intermediate depth and are regularly flooded by spring tides. This pattern in the present study is consistent with that of previous studies that have found deeper burrows in drier sediments (Takeda and Kurihara 1987; Wolfrath 1992; Lim and Diong 2003).

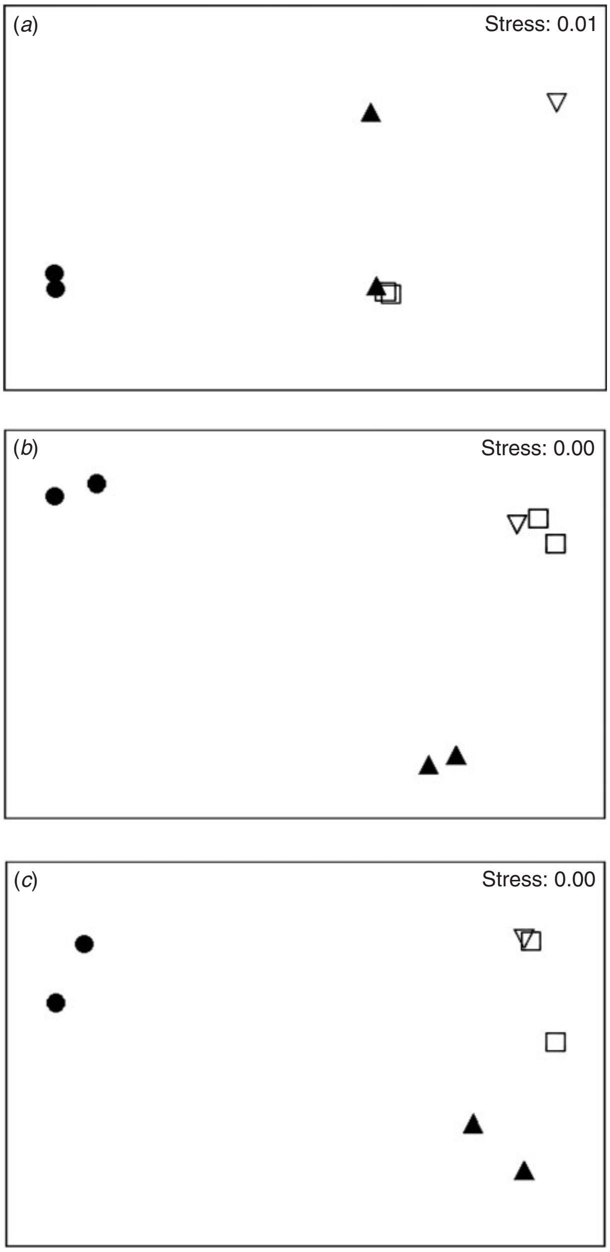

Fig. 4. Multi-dimensional scaling ordinations showing assemblages of burrows and different combinations of environmental variables. (*a*) Burrow assemblage, (*b*) non-dominant vegetation, % plant matter core and % very coarse sand in the entire core and (*c*) non-dominant vegetation and % very coarse sand at a depth of 10–15 cm. ▽, Goolwa; □, Port Noarlunga; ▲, Torrens Island; •, Middle Beach.

Table 4. Best fits of the BIOENV tests comparing the similarity matrix of burrow characteristics to the environmental variables of the entire core and by sediment depth

NDV, non-dominant vegetation; DV, dominant vegetation; pm, percentage of plant matter present in soil; st and vcs, percentage silt and very coarse sand in soil respectively; vcsA, percentage of very coarse sand present at a depth of 10–15 cm; vcsB, percentage of very coarse sand present at a depth of 15–20 cm; vcsC, percentage of very coarse sand present at a depth of 20–25 cm; vcsD, percentage of very coarse sand present at a depth of 25–30 cm

Entire core		Separate core depths	
Environmental variables	Spearman correlation	Environmental variables	Spearman correlation
NDV, vcs, pm	0.76	NDV, vcsA	0.83
NDV, vcs	0.75	NDV, vcsA, vcsB	0.82
NDV, vcs, DV	0.74	NDV, vcsB	0.82
vcs, DV	0.69	NDV, vcsA, vcsC	0.82
NDV	0.67	NDV, vcsA, vcsD	0.82
NDV, vcs, pm, DV	0.65	NDV, vcsA, vcsB, vcsC	0.82
NDV, vcs, DV, st	0.53	NDV, vcsA, vcsB, vcsD	0.82
vcs, pm	0.53	NDV, vcsC	0.80
NDV, vcs, pm, DV, st	0.52	NDV, vcsB, vcsC	0.80
NDV, vcs, st	0.50	NDV, vcsA, vcsC, vcsD	0.80

As with depth, the length of the burrow shafts differed significantly, with the longest burrows at Goolwa and the shortest at Middle Beach, whereas those at Port Noarlunga and Torrens Island were of intermediate length. This difference might be partly related to differences in the vegetation among the four sites. Previous studies on ocypodid crabs found that crabs preferentially dug burrows near hard structures, such as plants and experimental enclosures, because they provide the burrows with some structural support (Bertness and Miller 1984; Lim and Rosiah 2007). In the present study, the plant species that were present at Torrens Island and Goolwa had thicker root matter in the soil and unidentified, bulbous plant matter was found in the deeper sediments at Goolwa. The longer, more winding shafts observed at these two sites might result from the crabs having to dig around the plant matter present in the soil.

Despite a comparative lack of vegetation, the burrows at Middle Beach were more winding than those observed at Port Noarlunga, which were mostly straight shafts. The deeper layers of sediments at Middle Beach were coarser than those at a similar depth at the other sites, and this might have restricted deeper burrowing to some extent as burrowing in coarser sediments has a higher energy cost (Grow 1982). The comparative lack of below-ground plant matter would have enabled crabs at Middle Beach to easily dig further horizontally below the surface to increase the overall space available inside the burrow within a limited depth. The larger burrow volume and increased surface area would allow for a larger volume of air to aerate the water that collects in the burrow when submerged during high tide (Lim and Diong 2003). The more acute burrow angles resulting from this horizontal burrowing could also provide a better refuge from predators in the exposed areas (Lim and Heng 2007).

As threatened crabs usually retreat into the nearest burrow opening (Warren 1990; Morrisey *et al.* 1999), multiple entrances might allow for easy escape from predators. This would have been especially important at Middle Beach, which had more areas of exposed mud flat than the other three sites. Despite a higher level of vegetation cover and thus protection from avian predators, the burrows at Torrens Island had more entrances than the burrows at the other sites. An unidentified wolf spider, possibly from the genus *Hogna* (Araneae, Lycosidae), has been observed at the entrances of burrows and has been observed entering the same burrow as *H. haswellianus* at this site. Coastal species of wolf spiders are ground-dwelling ambush predators (V. Fremanau and D. Hirst, pers. comm.) and multiple entrances might provide the crabs with an alternative exit if a spider is present at one opening. Based on the behaviour of other lycosid spiders (Fairweather 1993; Marshall 1995; Framenau 2006), it is believed that these spiders are capable of at least a minimal amount of digging and could, potentially, expand the entrances of crab burrows to accommodate their larger size (V. Fremanau, pers. comm.). The presence of these large spiders at the burrow entrances would also explain why the burrow openings at Torrens Island were wider than those at the other sites.

While the burrow openings were the widest at Torrens Island, the burrow shafts were widest at Goolwa. Studies on the burrow morphology of the crab *Uca annulipes* (H. Milne Edwards, 1837) found that larger crabs generally excavated wider, more spacious burrows than small and medium-sized individuals (Lim and Diong 2003). In the present study, the greater width of the burrow shafts at Goolwa coincided with larger individual size of crabs in that population (median crab carapace width: 16.23 mm at Goolwa, 14.89 mm at Port Noarlunga, 13.52 mm at Torrens Island and 13.66 mm at Middle Beach; G. Katrak, unpubl. data). Chan *et al.* (2006) also found that adults of the ocypodid crab *Ocypode ceratophthalma* (Pallas, 1872) could tolerate longer periods of exposure to air by digging deeper and more complex burrows. Further studies are, however, needed to establish whether the larger crabs at Goolwa are better adapted to longer periods of exposure and if the sites have different age cohorts at any given time.

Each of the individual characters measured contributed to the overall 3D complexity of the burrows, represented by the fractal dimension D. The results of the fractal studies led to three groups of burrows based on their fractal dimension D: a group of highly complex burrows at Goolwa, a group of burrows of intermediate complexity at Middle Beach and Torrens Island, and a group of less complex burrows at Port Noarlunga. A higher burrow complexity can indicate greater available surface area underground, which is favourable for increased gas exchange and microbial colonisation (Thongtham and Kristensen 2003). This also allows organisms within the burrows greater access to resources in the surrounding environment. A simulation study on the fractal dimensions of burrows constructed by subterranean rodents and their foraging success found that, other environmental factors allowing, animals maximise foraging success by increasing burrow fractal dimensions (Le Comber *et al.* 2006).

Burrow complexity and burrow-opening density

The burrow-opening densities for each site gave no indication of the 3D complexity of the burrow morphology for that site in the present study. Despite significant differences in burrow-opening density within experimental areas, the burrows at both Middle Beach and Torrens Island were of intermediate complexity. The burrows at Goolwa were of high complexity, whereas those at Port Noarlunga were of low complexity, yet there were no significant differences in burrow-opening density between these two sites. Therefore, although burrow-opening counts might give an estimate of crab abundance at a site (MacFarlane 2002), they do not indicate the extent to which the sediments are used. Given the variation in burrow morphology seen for *H. haswellianus*, it is likely that burrow-opening counts are not an accurate indicator of crab abundance, particularly for comparisons between sites.

Burrow complexity and environmental variables

The present study revealed no clear pattern between vegetation parameters, sediment composition and the pattern of burrow morphology. This is in contrast to other studies that have found more straightforward relationships between similar environmental parameters and burrow complexity. No generalisation is possible between sediment grain size and crab burrow complexity; the mud crab *Helice crassa* (Dana, 1851) builds simple burrows in sandy sediments (Morrisey *et al.* 1999), whereas we found the most complex burrows for *H. haswellianus* in sandy sediments. Finer sediments might provide a more stable substrate for larger, more complex burrows owing to their more cohesive nature (Takeda and Kurihara 1987; Rudnick *et al.* 2005), yet burrows at the muddier sites in the present study were often simpler or of intermediate complexity. The presence of vegetation has been found to alter the stability of sediments (Bertness and Miller 1984). Therefore, the presence of vegetation in the present study could account for the differences observed in the patterns of burrow complexity and sediment type between *H. crassa* and *H. haswellianus*.

Roots and other plant matter in the sediments can interfere with burrow construction and increase the complexity of crab burrows, as the casts from Goolwa and Torrens Island demonstrated. Although Port Noarlunga and Middle Beach have similar sediments, the more exposed areas at Middle Beach might necessitate more horizontal digging and interconnectivity between burrows to provide better access to shelter from predators. A similar pattern was found for the ocypodid crab *U. annulipes*, which constructed burrows with significantly longer neck angles and horizontal lengths in bare habitats that might have provided better refuge from predators (Lim and Heng 2007; Lim and Rosiah 2007).

Although the saltmarsh vegetation at all four sites was dominated by *S. quinqueflora*, the dominant vegetation within one of the quadrats at Port Noarlunga was *S. australis*, whereas one of the quadrats at Middle Beach had no vegetation. The BIOENV results indicated that non-dominant vegetation is one of the factors influencing the differences in burrow morphology among sites. However, no significant differences in the fractal dimensions of the burrows were found between the two quadrats at either of these two sites. This suggests that the nature of the vegetation cover might have a limited effect within a certain area.

The lack of a simple link between the pattern of burrow morphology and the environmental variables recorded in the present study might result from the fact that other environmental factors, such as sediment compaction, temperature and the duration of exposure, are contributing to the differences observed in the burrow morphology. Biological factors, such as variation in crab population structure or associated fauna among sites, are also likely to be influencing burrow morphology. The complexity of burrows of the grapsid crab *Neoepisesarma versicolor* (Tweedie, 1940) was influenced by the burrowing behaviour of several generations of occupants as well as associated infauna (Thongtham and Kristensen 2003). Lim and Diong (2003) found that burrow morphology differed between males and females of *U. annulipes*. As the sexual dimorphism between male and female *H. haswellianus* is not as prominent as that observed in

U. annulipes, physical differences are unlikely to be as strong an influencing factor in the burrow morphology variation of *H. haswellianus* as they are for *U. annulipes*. However, behavioural differences cannot be discounted as a factor influencing burrow morphology variation because it is possible that male and female *H. haswellianus* use burrows for different purposes.

In conclusion, these results show that both sediment composition and vegetation cover do influence the morphology of *H. haswellianus* burrows. The various combinations of sediment type and vegetation as well as other environmental variables, such as inundation levels, result in burrows of varied complexity. More work is required to determine the extent of the influence of each of these environmental factors on burrow morphology at different spatial or regional scales, but the destructive nature of burrow casting, particularly when excavating larger, more complex burrows, is a limiting factor in obtaining large sample sizes. However, the spatial variation in burrow morphology found in the present study suggests that the ecosystem engineering functions of this species will vary between areas with differing vegetation and sediment composition and are likely to be site specific, and this is currently being addressed in further studies.

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