DENSITIES AND APERTURE SIZES OF BURROWS CONSTRUCTED BY *HELOGRAPSUS HASWELLIANUS* (DECAPODA: VARUNIDAE) IN SALTMARSHES WITH AND WITHOUT MOSQUITO-CONTROL RUNNELS

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Abstract: The relationship between environmental factors and the spatial distribution of maintained and actively used burrows of the grapsid crab *Helograpsus haswellianus* was studied at three saltmarsh sites in southeast Queensland, Australia. The sites had been modified by runnelling for mosquito-control, a method that transports low-amplitude tides to areas of saltmarsh. The study investigated the relationship between burrow density, burrow aperture size, and runnelling, as well as the effect of flooding or non-flooding tides and distance from a tidal source. Responses differed at the three sites. The most consistent pattern across all sites was that active burrows were most numerous between 30 and 50 m from the saltmarsh / mangrove interface at the landward side of the tidal source. At particular sites, there were significant relationships between burrow aperture size, tidal period, and the presence of runnels. Generally, few small burrows occurred low on the shore, while larger burrows were distributed across the shore to 50 m. At naturally dry sites, more burrows occurred within 5 m of the runnel, whereas at naturally wet sites, fewer burrows were found close to the runnel. As runnels transport low-amplitude tides, moisture conditions required for burrowing may very between flooding and non-flooding tides. Overall, the influence of tides on the density of crab burrows and their aperture sizes was of more importance than the presence of runnels alone.

Key Words: Australia, crustaceans, tidal frequency, habitat modification, intertidal wetland

INTRODUCTION

The shore crab *Helograpsus haswellianus* White-legge (Decapoda: Varunidae) (Schubart et al. 2002) is common on saltmarshes in southeastern Australia from Queensland to South Australia and Tasmania (Fielder and Greenwood 1984). The crab is nocturnal, euryhaline, and forages on intertidal substrates during low tide. *Helograpsus haswellianus* has morphological features characteristic of terrestrial land crabs, such as high gill volume to body ratio, walking hind legs, and hairs between the walking legs to reduce water loss (Griffin 1966), but it does not commonly inhabit areas devoid of tidal influence. Rather, *H. haswellianus* oc-

cupies the highest shore positions of marine crab species (Griffin 1971), from the upper midlittoral into the supralittoral fringe (McKillup and Butler 1979). Generally, Australian saltmarshes occur at higher shore elevations and are inundated by tidal waters for shorter periods than marshes on the east coast of the USA. The position of Australian saltmarshes in the intertidal zone provides extensive areas for crab burrowing and may explain the diversity of species present.

Helograpsus haswellianus constructs burrows for protection from predation and desiccation and for breeding and moulting (Dunham and Gilchrist 1988, Morrisey et al. 1999). Burrows extending to depths of 30–40 cm are regularly maintained by the resident crab

(Marsh 1982). Burrow aperture is close to the size of resident crabs, and maintenance involves movement of soil from the lowest regions of the burrow to the opening at the surface, thereby creating a cycle of bioturbation (Dunham and Gilchrist 1988). This process occurs after tidal inundation and releases small quantities of anoxic and oxic sediments that facilitate soil metabolism and oxidation by reducing the accumulation of toxic substances (Marsh 1982). Infrequent inputs of seawater (percolating up from the water table or from flooding tides) further neutralize soil chemicals and are critical in the health of intertidal systems undergoing anthropogenic influence (Williamson et al. 1999).

Freshly constructed and regularly maintained burrows of *H. haswellianus* are readily distinguished from abandoned ones (Breitfuss 2003). Although abandoned burrows may persist for long periods on saltmarsh they can be differentiated from the actively maintained ones by the lack of fresh sediment deposits at the entrance and the degree of wear to the burrow entrance. Abandoned burrows appear not to be recolonized by *H. haswellianus* (Breitfuss 2003). The separation of burrows based on use greatly increases the accuracy of employing burrow counts for estimating the abundance of *H. haswellianus* on saltmarsh (Breitfuss 2003).

The greatest densities of burrows constructed by *H. haswellianus* usually occur in drier substrate and seldom occur in waterlogged soils (Higginbottom 1982, Marsh 1982). Soil-water content has been associated with crab burrowing, and *H. haswellianus* is reported to avoid wet conditions, favoring well-drained substrates (Marsh 1982, Richardson et al. 1997). In Tasmania, preferred soil conditions allow the species to construct burrows close to the source of tidal waters (Richardson et al. 1998), whereas in Queensland, these conditions can restrict high-density burrowing to distances greater than 30 m landward from the saltmarsh / mangrove interface at the shore (Chapman et al. 1998). In Queensland saltmarsh, the main source of tidal water (usually a creek, bay or river) can be at some distance from the saltmarsh / mangrove interface, so incoming and ebbing tides tend to follow slight depressions in the mangrove before reaching the saltmarsh.

Runnelling is a physical habitat modification technique for mosquito control in saltmarsh. The method involves linking isolated mosquito-breeding pools to slight depressions at the saltmarsh / mangrove interface via shallow (<30 cm deep), spoon-shaped channels, thereby increasing the frequency of tidal inundation to runnelled areas of the high marsh (Breitfuss et al. 2003). As a result of runnelling activities, tides with amplitudes up to 25 cm less than that which would normally flood saltmarsh are transported. It is reported that there is an associated increase in the
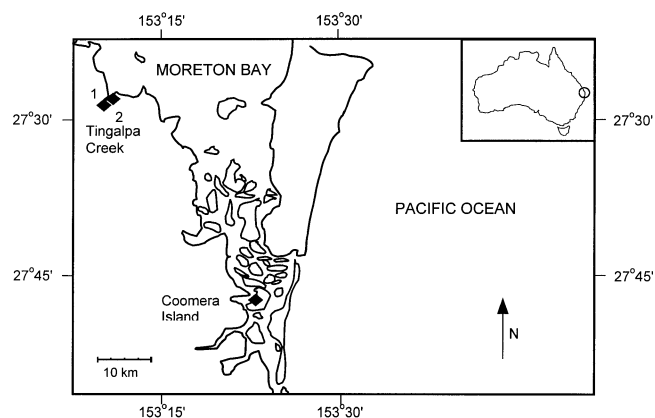

Figure 1. Location of saltmarsh sites (black diamonds) in southern Moreton Bay.

moisture content of saltmarsh soils adjoining the runnel (Hulsman et al. 1989), and these levels can be sustained for periods following tidal ebb (Breitfuss and Connolly 2004). Mosquito control is achieved by increasing flushing of breeding pools and enabling increased predator access to the pools (Hulsman et al. 1989).

Runnelling is a popular and efficient method of reducing mosquito larval densities in saltmarsh; however, specific non-target impacts of the method have not been investigated. Given the substrate conditions necessary for burrowing by *H. haswellianus*, runnelling may influence the distribution of these crabs. If runnels cause soil characteristics to change beyond the range of tolerable conditions for maintenance of burrows, this may be evident in comparative differences in the density of actively used burrows between sites with and without runnels. Further, changes in the population dynamics of the species may be reflected in the structure of burrow aperture size classes. Therefore, the aim of this study was to examine the relationship between the spatial distribution of crab burrows, their aperture size, and the presence of runnels.

METHODS

Study Sites

Density and aperture of burrows of *Helograpsus haswellianus* were measured in three saltmarsh shores (hereafter called sites) in southern Moreton Bay, southeast Queensland, Australia (Figure 1) between March 2000 and December 2001. The three sites (Coomera, Tingalpa 1, and Tingalpa 2) had a similar tidal range (approximately 2.5 m) and relative relief (approximately 0.5 m) but not vegetation dominance.

The Coomera site was largely composed of the saltmarsh grass, *Sporobolus virginicus* (L.) Kunth, with few patches of succulent glasswort, *Sarcocornia quin-*

queflora (Bunge ex Ung.-Sternb.) A.J. Scott, whereas Tingalpa 2 was composed of only the succulent glasswort. Tingalpa 1 site was a mosaic of both species with neither dominating. Other saltmarsh herbs such as *Suaeda australis* (R. Br.) Moq. were present but patchily distributed and not common. Although the saltmarsh vegetation differed in terms of composition at each site, its extent on the shore was similar, being bounded at the lowest shore height by mangrove community, composed of *Avicennia marina* var. *australasica* (Walp.) J. Everett.

Study Animals and Definition of Burrow
Characteristics

A number of crabs are common in intertidal habitats, with species representing grapsoids, portunids and ocypodids. In general, grapsoids have terrestrial adaptations and lack the paddle hind leg of portunids, which are rare on saltmarsh, although some commercial species (*Scylla serrata* Forsskal and *S. olivaceae* Herbst) do burrow on lower shore fringes. Ocypodids also inhabit lower regions and are common on exposed mudflats and mangrove.

Although burrowing by *H. haswellianus* was the focus of this study, two other crabs were common, which required that their burrows be distinguished from those of the target species. *Australoplax tridentata* A. Milne Edwards (Ocypodidae) and *Sesarma erythodactyla* Hess (Grapsidae) occur within the intertidal limits of *H. haswellianus* and burrow in similar substrate (Snelling 1959). *Sesarma erythodactyla* tends to burrow in wetter substrates and may overlap in distribution with *H. haswellianus*. Similarly, *A. tridentata* is common on exposed mudflats at the saltmarsh/mangrove interface and other areas of saltmarsh that sustain wet or waterlogged conditions (Snelling 1959) within the range of *H. haswellianus*.

Only burrows that were obviously maintained were censused in this study. Specific criteria included signs of fresh workings around the burrow entrance, minimal degradation of the entrance, maintenance of substrate between multiple entrances, and aperture not exceeding chamber diameter. Burrow aperture reflects the actual size of resident crabs (Dunham and Gilchrist 1988) and was measured using vernier calipers. Aperture comprised the maximum inside diameter of the entrance from edge to edge (burrows are not necessarily circular and may be ovoid in shape). Recorded burrow apertures were grouped into six size classes 0–5, 6–10, 11–15, 16–20, 21–25, and 25+ mm, which was believed to reflect actual sizes of resident crabs.

Crabs responsible for burrow construction and maintenance were identified by visual identification of resident species inhabiting the burrow. An understanding of burrowing habits of resident species reduced the effort required for identification. For example, *A. tridentata* constructs shallow burrows, with resident crabs found close to the surface (often within 2 cm of burrow entrance). *Sesarma erythodactyla* and *H. haswellianus* may inhabit similar regions of saltmarsh but have different circadian rhythms and feeding preferences (Griffin 1966). *Helograpsus haswellianus* is rare on open ground during the day, whereas *S. erythodactyla* will feed on algal deposits following daytime high tides. When foraging, *S. erythodactyla* may use the burrow for rest periods, during which time it remains high in the chamber and is easily extracted for identification. Extraction of *A. tridentata* and *S. erythodactyla* involved pushing a long skewer into the burrow behind the crab so that the resident would move towards the entrance and capture.

Sampling Design

Actively used crab burrows and aperture features were sampled from 25 × 25 cm quadrats using two experimental design protocols (Figure 2). For the first sampling protocol, two 50-m (continuous 10 × 10 m plots) transects were established, one along the runnel and the other 20 m from and parallel to the runnel (Figure 2). Within each plot, ten randomly selected quadrats were selected and burrow density and aperture sizes taken from each quadrat. The beginning of the transects was set on the seaward edge of the saltmarsh at the saltmarsh/mangrove interface. The first sampling protocol compared differences in burrow density for each aperture size between parallel transects where one transect encompasses the runnel. Five shore heights were included in the comparison to identify variation with distance from the tidal source.

For the second sampling protocol (Figure 2), transects were located at right angles to the runnel at distances of 0, 30, and 50 m up the shore, from the inland edge of the saltmarsh/mangrove interface. Sampling quadrats were situated along each transect at nine distances (from 0–20 m) from the runnel edge in both directions (Figure 2) and burrow features measured. The second sampling protocol provides evidence for the extent of any change with distance from the runnel edge. The inclusion of three shore heights enables comparisons of variation with distance from the tidal source.

Burrow features were sampled approximately one hour after a predicted (Queensland Department of Transport 2001) spring high tide that was either a non-flood (2.25–2.38 m) or flood (2.42–2.56 m) event. Flooding events persisted for a period of 3–4 days during each sampling episode, and each site was sampled once for a non-flood and flood event. Non-flood tides
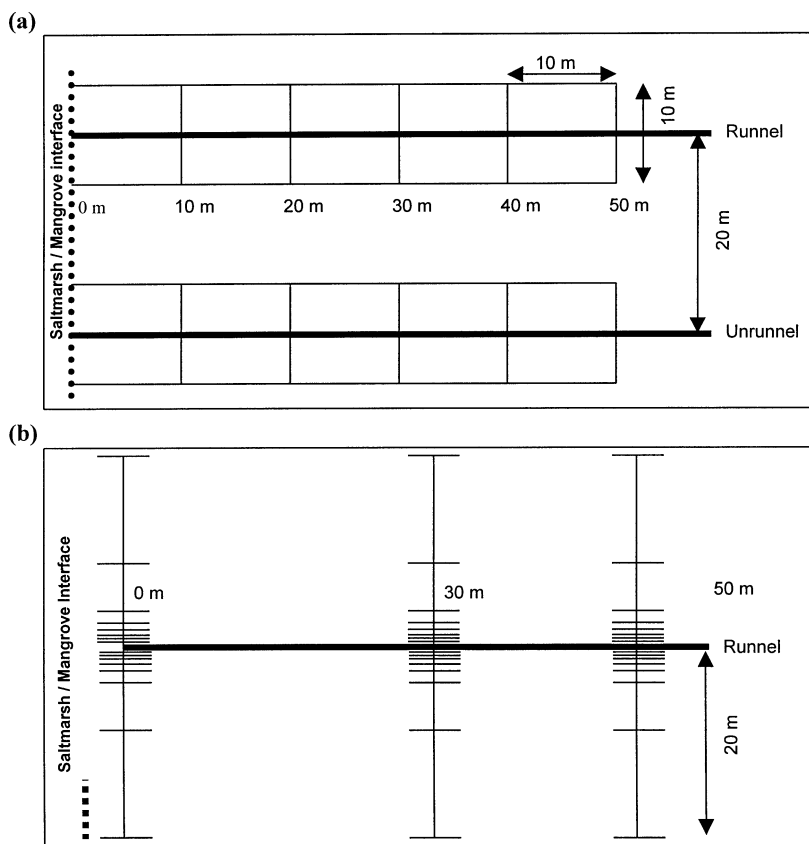
Figure 2. Sampling design and plot dimensions for (a) first sampling protocol comparing runnelled and unrunnelled transects and (b) second sampling protocol showing lateral spread of sample points from the runnel edge (0.5, 1, 1.5, 2, 2.5, 3, 5, 10, 20 m) at three shore heights.

in the range of 2.25–2.38 m accounted for approximately 16% of annual tidal events and reached the saltmarsh-mangrove interface but did not inundate the saltmarsh, except for areas contained within runnels. Tidal flood events accounted for approximately 7% of annual tides and breached the saltmarsh, extending at least 50 m up the shore onto the saltmarsh. Tidal period was considered important in comparing the density of burrows between the runnel and unrunnelled sites, with the prediction being that the runnel would have features more similar to flood events than non-flood.

Data Analyses

Separate ANOVA tests for each aperture size class were used to detect differences in densities of burrows. For sampling protocol 1, an orthogonal 3-way ANOVA was used where tide (flooding, non-flooding), distance from the saltmarsh / mangrove interface (hereafter called shore height, with 5 levels), and treatment (runnelled or unrunnelled) were fixed factors (n = 10 quadrats in each combination of the three factors). Data were tested for departures from homoscedastici-

ty; no transformations were required. Burrow densities from the second protocol were analyzed with 3-way ANOVA where tide, shore height, and distance from runnel edge were fixed factors. Data from transects on both sides of the runnel were pooled so that the analysis concentrated on consistent differences with distance from the runnel (n = 4 quadrats in each combination of the three factors). Pooled data were tested for honoscedasticity and required no transformation prior to ANOVA. Tukey tests (HSD) were used to identify differences among means. Data from the three marshes were analyzed separately.

RESULTS

At Coomera, the interaction of tide and treatment significantly influenced the density of actively used burrows (Table 1), with fewer recorded at the runnel transect after flooding tides than non-flooding tides (Figure 3). There was little change in the density of burrows at the unrunnelled transect with tidal amplitude alone.

The presence of runnels weakly influenced the density and distribution of 6–10 mm sized burrows at the

Table 1. Summary of three-way ANOVA results on burrow density for all aperture size classes combined and individually of crabs at runnelled and unrunnelled transects. Only significant results are shown.

Site	Factor	df	P
All aperture size classes combined			
Coomera	treatment	1	**
	tide × treatment	1	***
Tingalpa 1	tide	1	*
By aperture size class			
Coomera	*6–10 mm*		
	treatment	1	*
	tide × treatment	1	**
	11–15 mm		
	treatment	1	***
Tingalpa 1	*6–10 mm*		
	tide	1	*
	tide × treatment	1	**
	16–20 mm		
	tide	1	*
	treatment		*
	21–25 mm		
	treatment	1	*
Tingalpa 2	*16–20 mm*		
	tide	1	*
	21–25 mm		
	tide	1	*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

runnelled transect, which were more similar in number to the unrunnelled transect after a flood tide (Figure 3). A stronger pattern was evident for 11–15 mm wide burrows which were always more common at the runnel compared to the unrunnelled transect (Table 1, Figure 3).

Tide was an important factor influencing the distribution of actively used crab burrows at Tingalpa 1, with more burrows recorded lower on the shore from unrunnelled transects than runnelled ones after both tidal events (Figure 3). Burrows in the size range 6–10 mm were more common at the unrunnelled transect after non-flooding tides but were absent after flooding events, while the distribution at the runnel remained similar after both tidal periods (Table 1, Figure 3). Burrows in the range 16–20 mm were more abundant at the runnel transect after a non-flooding tide than a flooding tide, whereas those on the unrunnelled transect were similar regardless of the tidal amplitude. Large burrows in the 21–25 mm class were not recorded during non-flood tides but were common on the unrunnelled transect after flooding events (Figure 3).

Tide weakly influenced the distribution of burrows at Tingalpa 2. Fewer of the 16–20 mm sized burrows were recorded on the unrunnelled transect after flood-ing tides, whereas those in the 21–25 mm range were common at both transects after flooding tides (Table 1, Figure 3).

At Coomera, density and distribution of actively used burrows along lateral distances from the runnel edge were strongly influenced by tidal period, shore height, and their interaction. The numbers of burrows at the shore heights are different from each other and these differences change with respect to the tidal period measured (Table 2). Small burrows in the range of 6–10 mm were always more common lower on the shore after both tidal periods while larger 21–25 mm sized-burrows were more common at higher shore positions for the same tides.

Tidal period influenced burrows in the mid-sized ranges 11–15 mm and 16–20 mm, which were rare following flooding tidal periods (Table 2). Lateral distance from the runnel edge did not significantly influence burrow density, although more burrows were generally recorded at 30 m and 50 m shore heights and within 5 m of the runnel after both tides (Table 2).

At Tingalpa 1 and Tingalpa 2, more larger used burrows were recorded at mid-shore heights and closer to the runnel after both tidal periods whereas small burrows tended to be more common across all positions low on the shore (Table 2). However, 6–10 mm burrows at Tingalpa 2 were common at low and mid-shore heights, beyond 2 m of the runnel edge, and after non-flood tides (Table 2). The distribution of these small burrows accounted for much of the general pattern at Tingalpa 2.

DISCUSSION

Smaller actively used burrows tended to dominate at the runnel transects. However, the presence of runnels seemed to have little impact on the distribution of burrows at the three sites. Also, while there were some differences between runnelled and unrunnelled transects, or interactions between treatment and tide, the patterns were not very strong. Tidal period was a more important factor, with increased density of larger used burrows at the runnel following flooding tides and fewer mid and large burrows at the unrunnelled transect for the same tide. The associated influence of the runnel and tidal period on substrate burrowing conditions is worth further consideration, as this interaction could be responsible for observed patterns, rather than the effect of each factor individually. Skilleter and Warren (2000) reported similar patterns for *Sesarma erythodactyla* and *Helograpsus haswellianus* burrowing in disturbed substrate in mangrove forests, noting increased burrow density where soil conditions apparently favored burrow construction.
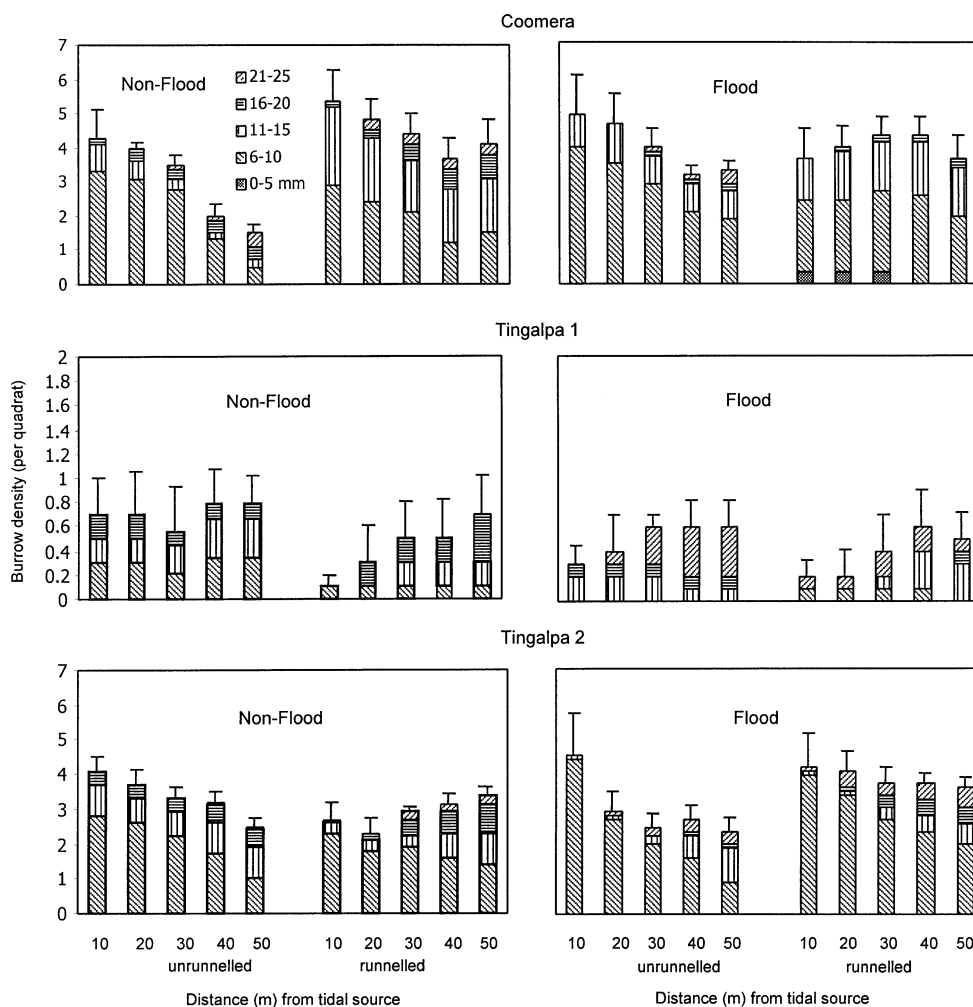
Figure 3. Stacked histograms of aperture density, showing means for each size class of active burrows constructed by *Helograpsus haswellianus* along unrunnelled and runnelled transects after non-flooding and flooding tides at three saltmarsh sites. The y-axis of Tingalpa 1 is re-scaled to highlight patterns. Error bars are Standard Errors for overall means (all size classes pooled), n = 10 for each individual size class mean.

The overall density of actively used burrows at Coomera was influenced by the presence of runnels, but particular aperture size classes may reflect broader hydrologic processes described by Breitfuss et al. (2003). Specifically, crabs responsible for constructing mid-sized burrows in the range 11–15 mm may be able to exploit additional burrowing habitat in the vicinity of the runnel. This is associated with increased soil-water content of runnel substrate (Hulsman et al. 1989) following non-flooding tides, which may offer better conditions for crab burrowing (Snelling 1959, Richardson et al. 1998) compared to the unrunnelled transect which remains dry for tides other than flooding events.

The substrate at Tingalpa 1 is susceptible to extreme changes in consolidation and moisture content, regardless of the presence of the runnel (Breitfuss, unpublished data). Natural variation in the density of actively

used burrows at the unrunnelled transect between tidal periods supports this, and runnelling may simply exacerbate already erratic patterns. It is likely that runnels remove available moisture from lower shore sediments, thus reducing suitable burrowing habitat. At these lower shore regions, flooding tides are required for the construction of larger burrows (Marsh 1982), which were recorded only after these events. Alternatively, the disappearance of small 6–10 mm burrows at the unrunnelled transect between tidal periods may reflect sub-surface increases in moisture content, which provide an advantage for burrowing of larger crabs (Snelling 1959, Griffin 1971). At Tingalpa 1, the presence of the runnel may reduce natural soil-water fluctuation resulting in more stable burrowing conditions between tidal periods.

Small and mid-sized used burrows comprised the majority of records at all shore heights measured at

Table 2. Summary of three-way ANOVA results on burrow density for all aperture size classes combined and individually of crabs at lateral distances from the runnel edge. Only significant results are shown. Tukey's HSD results are shown where significant factor has greater than two levels. Group means are presented in ascending order.

Site	Factor	df	P	Tukey†
Coomera	tide	1	***	
	shore	2	***	3[a] 2[b] 1[c]
	tide × shore	2	***	
Tingalpa 1	shore	2	***	1[a] 2[b] 3[c]
	distance	7	**	1[a] 8[a] 7[ab] 5[ab] 2[ab] 3[ab] 6[bc] 4[c]
Tingalpa 2	tide	1	***	
	shore	2	***	3[a] 2[b] 1[b]
	distance	7	**	2[a] 3[a] 7[a] 4[a] 8[ab] 5[ab] 6[ab] 1[c]
By aperture size class				
Coomera	*6–10 mm*			
	shore	2	**	3[a] 2[ab] 1[bc]
	11–15 mm			
	tide	1	*	
	16–20 mm			
	tide	1	**	
	21–25 mm			
	shore	2	**	1[a] 2[ab] 3[bc]
Tingalpa 1	*6–10 mm*			
	tide	1	**	
	shore	2	*	1[a] 2[ab] 3[bc]
	tide × distance	7	*	
	11–15 mm			
	shore	2	*	1[a] 2[b] 3[b]
	distance	7	***	
	16–20 mm			
	tide		*	
	shore	2	***	1[a] 2[b] 3[b]
Tingalpa 2	*6–10 mm*			
	tide	1	***	
	shore	2	***	3[a] 2[b] 1[c]
	distance	7	**	7[a] 3[a] 2[a] 4[a] 6[ab] 8[ab] 5[ab] 1[c]
	tide × shore	2	*	
	11–15 mm			
	tide × shore	2	*	
	16–20 mm			
	tide	1	**	
	shore	2	*	1[a] 2[ab] 3[bc]
	distance	7	*	2[a] 3[a] 8[a] 1[ab] 7[ab] 4[ab] 5[ab] 6[c]
	tide × distance	7	**	
	21–25 mm			
	distance	7	*	1[a] 2[a] 3[a] 4[a] 5[a] 6[a] 8[a] 7[b]

† Dissimilar superscript denotes sig. diff. ($P < 0.05$) between subsets; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

lateral distances from the runnel edge on the Coomera site. However, small crabs may extend further up the saltmarsh shore only after flooding tides because substrate conditions would usually restrict their burrowing to softer sediments lower on the shore. This pattern was discussed by Chapman et al. (1998) in terms of patches of suitable burrowing habitat that may be promoted or reduced by some physical activities that alter soil-water availability. It is possible

that the influence of flooding tides on soil-water content extends beyond the edge of the runnel, thus enabling smaller crabs to burrow at greater lateral distances from the runnel (which acts as a source of soil moisture) than may occur in the absence of the structure. Chapman et al. (1998) described the runnel as promoting low marsh features into the high marsh. At Coomera island, Chapman et al. (1998) described colonization of runnels by *Australoplax*

tridentata, a low marsh species common on the salt-marsh/mangrove interface.

The pattern of crab burrowing at Tingalpa 1 strongly supports those from the previous section, with few burrows recorded low on the shore. Mid- and larger sized burrows tended to dominate the overall distribution close to the runnel edge. This may be because sediment within 5 m of the runnel receives moisture inputs (Chapman et al. 1998, Dale et al. 1998) that make it more suitable for crab burrowing compared to greater distances from the runnel. While this range of conditions may increase burrowing at a naturally dry site like Tingalpa 1, the stability of conditions required for larger crabs to burrow (Snelling 1959) at other saltmarshes could result in their avoidance of overly wet soils (Marsh 1982).

Site heterogeneity is implicit in the explanation of patterns for crab burrowing. Although runnelling does have some influence on the availability of suitable habitat for species, it is unlikely to cause changes in community composition at levels of significance other than local scales (see discussion by Dale and Dale 2002). Crabs probably respond to subtle changes in substrate characteristics that affect their burrowing, so runnelling may simply exacerbate processes already occurring. The increase of inundation frequency near runnels may reduce burrowing opportunities for mid-sized crabs, whereas small and large crabs are not influenced greatly. Also, it is possible that some size classes were absent from samples because of the interval between tides. For example, the 6–10 mm size class way be absent from flood samples at Tingalpa 1 because this site was sampled long enough after the previous non-flood tide to allow these animals to grow and become the 11–15 mm size class.

SUMMARY

Although the results show variation in actively used crab burrow distribution between sites, the greatest number of active crab burrows were generally at the mid-shore distance 30–50 m from the saltmarsh / mangrove interface. The variation between sites was greatest in the effect of tidal condition and distance from runnel. Thus, there were larger numbers of burrows at the Coomera site in the runnelled area on non-flooding rather than flooding tides, whereas at Tingalpa 1, there were fewer burrows associated with runnels regardless of flooding. Distance from runnel was also an important factor, although not a simple one, as larger numbers were found beyond 2 m from the runnels at the site, with *Sarcocornia* dominant but within 5 m from the runnels at the site predominantly of *Sporobolus*.

There were interactions between runnelling and flooding and non-flooding tides, but these differed between sites. Size of burrow also differed significantly between sites and may be related to sediment characteristics such as soil moisture and consolidation, which are significantly influenced by runnels (Breitfuss and Connolly 2004). Overall the results indicate that each site is different and that this heterogeneity makes it difficult to generalise.

ACKNOWLEDGMENTS

LITERATURE CITED

Breitfuss, M. J. 2003. Defining the characteristics of burrows to better estimate abundance of the grapsid crab, *Helograpsus haswellianus* (Decapoda, Grapsidae), in an Australian saltmarsh. Crustaceana 76:499–507.

Breitfuss, M. J. and R. M. Connolly. 2004. Consolidation and water content of coastal saltmarsh substrates following mosquito control habitat modification. Wetlands Ecology and Management (in press).

Breitfuss, M. J., R. M. Connolly, and P. E. R. Dale. 2003. Mangrove distribution and mosquito control: transport of *Avicennia marina* propagules by mosquito control runnels in southeast Queensland saltmarshes. Estuarine Coastal and Shelf Science 56:573–579.

Chapman, H. F., P. E. R. Dale, and B. H. Kay. 1998. A method for assessing the effects of runneling on salt marsh grapsid crab populations. Journal of the American Mosquito Control Association 14:61–68.

Dale, P. E. R., A. L. Chandica, and M. Evans. 1996. Using image subtraction and classification to evaluate change in subtropical intertidal wetlands. International Journal of Remote Sensing 17: 703–719.

Dale, P. E. R. and M. B. Dale. 2002. Optimal classification to describe environmental change: pictures from the exposition. Community Ecology 3:19–29.

Dunham, D. W. and S. L. Gilchrist. 1988. Behaviour. p. 97–138. *In* W. W. Burggren and B. R. McMahon (eds.) Biology of the Land Crabs. Cambridge University Press, Cambridge, UK.

Fielder, D. R. and J. G. Greenwood. 1984. The complete larval development of *Helograpsus haswellianus* (Whitelegge) (Decapoda, Grapsidae), reared in the laboratory. Proceedings of the Royal Society of Queensland 95:11–22.

Griffin, D. 1966. The taxonomy, ecology and social behaviour of the Tasmanian shore crabs (Crustacea, Brachyura) of the families Grapsidae and Ocypodidae. Ph.D. Dissertation. University of Tasmania, Tasmania, Australia.

Griffin, D. 1971. The ecological distribution of grapsid and ocypodid crabs (Crustacea: Brachyura) in Tasmania. Journal of Animal Ecology 40:597–621.

Higginbottom, K. B. 1982. Behavioural ecology of the mud crab *Helograpsus haswellianus*: agonistic behaviour and burrows. Honours Thesis. University of Adelaide, Adelaide, Australia.

Hulsman, K., P. E. R. Dale, and B. H. Kay. 1989. The runnelling method of habitat modification: an environment-focussed tool for salt marsh mosquito management. Journal of the American Mosquito Control Association 5:226–234.

Marsh, J. 1982. Aspects of the ecology of three saltmarshes of the Derwent region, and an investigation into the role of the burrowing crab *Helograpsus haswellianus* (Whitelegge, 1889). Honours Thesis. University of Tasmania, Tasmania, Australia.

McKillup, S. and A. Butler. 1979. Cessation of hole-digging by the crab *Helograpsus haswellianus*: Resource-conserving adaptation. Marine Biology 50:157–161.

Morrisey, D., T. H. De Witt, D. Roper, and R. Williamson. 1999. Variation in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediment in New Zealand. Marine Ecology Progress Series 182:231–242.

Queensland Department of Transport. 2001. The Official Tide Tables and Boating Safety Guide 2001. Queensland Department of Transport, Brisbane, Australia.

Richardson, A. M. M., R. Swain, and V. Wong. 1997. The crustacean and molluscan fauna of Tasmanian saltmarshes. Proceedings of the Royal Society of Tasmania 131:21–30.

Richardson, A. M. M., R. Swain, and V. Wong. 1998. Relationship between the crustacean and molluscan assemblages of Tasmanian saltmarshes and the vegetation and soil conditions. Marine and Freshwater Research 49:785–799.

Schubart, C. D., J. A. Cuesta, and D. L. Felder. 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. Journal of Crustacean Biology 22:28–44.

Skilleter, G. and S. Warren. 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. Journal of Experimental Marine Biology and Ecology 244:107–129.

Snelling, B. 1959. The distribution of intertidal crabs in the Brisbane River. Australian Journal of Marine and Freshwater Research 10:67–83.

Williamson, R. B., R. J. Wilcock, B. E. Wise, and S. E. Pickmere. 1999. Effect of burrowing by the crab *Helice crassa* on chemistry of intertidal muddy substrates. Environmental Toxicology and Chemistry 18:2078–2086.