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INVESTIGATING GASTROPOD HABITAT ASSOCIATIONS IN SALTMARSH

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ABSTRACT

Recent studies have provided new information on the taxonomy of gastropods snails in Australian saltmarsh but little is known of their ecology. For fauna colonisation to be used as a measure of the success of restoration or rehabilitation of degraded saltmarsh, a detailed understanding of the microhabitat associations of the target species in 'reference' locations across a range of latitudes is necessary. This study measured the densities of saltmarsh gastropods in two locations in northern New South Wales to determine microhabitat associations that could influence the results of rehabilitation assessment using fauna colonisation in Australian saltmarsh. In this study, *Ophicardelus* spp. were common in tall vegetation, in particular, *Juncus kraussii. Phallomedusa solida* was commonly on mud substrates but was more evenly distributed across the saltmarsh than *Ophicardelus ornatus.* This study has implications for the design and assessment of restoration projects. If habitats of the individual species are not created by rehabilitation actions, or do not occur for whatever reason, densities of particular species will be lower than at reference sites, thus influencing assessment of the 'success' of saltmarsh rehabilitation using gastropod snails.

Key words: habitat, gastropods, Juncus kraussii, saltmarsh, pulmonate gastropods

INTRODUCTION

The pulmonate gastropods from the Ellobiidae, the Amphibolidae (air-breathing gastropods), and the Littorinidae (periwinkles) are dominant molluscs in Australian east coast saltmarsh (Smith and Kershaw 1979; Kaly 1988; Roach and Lim 2000; Hyman *et al.*, 2004). Although identification of saltmarsh gastropods occurred early in colonial Australian history, more detailed studies of the taxonomy of the species were limited until recently. This lack of taxonomic information limited the potential for ecological studies (Hyman *et al.*, 2004; Golding *et al.*, 2007).

Gastropod distribution within sites depends on habitat, shelter, food, predation and competition (Kaly 1988, Breitfuss 2003). Recent work on the ecology of the individual species has provided good foundations for the development of the use of gastropods as a measure of ecological change in eastern Australian saltmarsh (Kaly 1988; Richardson, Swain and Wong 1998; Breitfuss 2003). These studies have tested and evaluated suitable gastropod sampling procedures for saltmarsh studies and generated evidence for future testing of specific hypotheses in relation to gastropod microhabitat associations.

Densities of *Ophicardelus* spp. appear to be lower near the mangroves and higher in saltmarsh (Breitfuss 2003). *Phallomedusa solida*, *Cryptassiminea tasmanica* and *Ophicardelus* spp. have been identified as predominantly saltmarsh species and do not appear to move up or down the elevation gradient into other zones (Kaly 1988). Kaly (1988) Laegdsgaard (2006), Ross *et al.* (2009) have all reported that *Ophicardelus* spp. appear to have some association with *Juncus kraussii.* Warren (1985) suggests that gastropod species use the stems of the tall grass, *Spartina alterniflora*, as an effective method to escape predation during high tides, but experiments in Darwin Harbour confirmed that molluscs climb to avoid physiological stress during neap tides (McGuinness 1994). The saltmarsh periwinkle, *Littoraria irrorata*, feeds on the substrate at low tide, but is inactive in winter and aggregates with other snails at the base of *Spartina* clumps in detrital matter (Vaughn and Fisher, 1992).

A detailed understanding of the individual species microhabitat associations is required before the organism can be used as a monitoring and assessment tool. Previous studies have indicated microhabitat associations for saltmarsh gastropods (Richardson *et al.*, 1998; Armitage and Fong, 2004), but evidence was not conclusive. Some studies have reported an apparent association between some gastropods species and individual saltmarsh vegetation types (Richardson *et al.*, 1998, Laegdsgaard 2006).

The aim of this study was to test the hypothesis that saltmarsh gastropods have distributions related to saltmarsh vegetation that may affect the interpretation of the results of assessment of fauna abundances. This study was considered an essential component for development of programs for the measurement of the success of saltmarsh restoration using gastropod density as a measure.

METHODS

Study Sites

The habitat associations of the pulmonate gastropods were investigated at two locations, Brunswick Heads and Fingal Peninsula (Figure 1). Fingal Peninsula (28° 10.350’S 153° 33.307’E) forms the south headland of the mouth of the Tweed River, on the border between Queensland and New South Wales. Brunswick Heads is south of Fingal Peninsula (29° 23.406’S, 153° 20.954’E) and contains one of the largest areas of remaining saltmarsh in the Brunswick River catchment. Brunswick Heads was the major focus site for this study.

Study sites were chosen within these locations which represented a ‘non-disturbed’ or reference saltmarsh community of northern New South Wales. A reference community would typically provide a comparison for studies of flora and fauna colonisation after saltmarsh restoration works and would therefore be a desirable goal for a successful saltmarsh restoration project. A saltmarsh reference community was defined as one with an intact soil profile and saltmarsh vegetation cover with little or no obvious evidence of disturbance

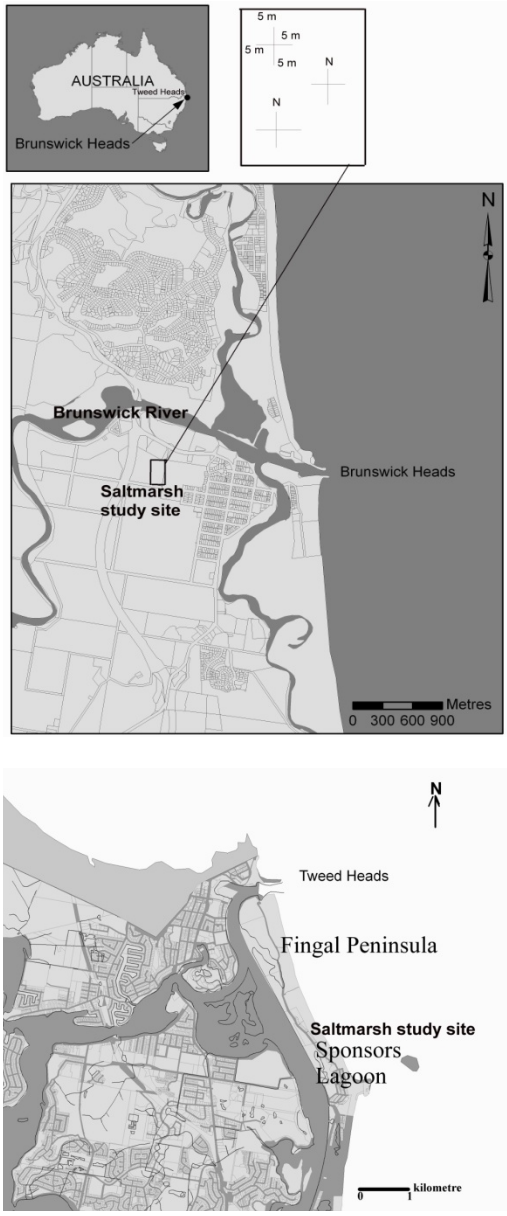

Figure 1 –Location of the study sites, Brunswick Heads and Fingal Peninsula in northern New South Wales and Australia.

from vehicles, stock, or other human activity.

Saltmarsh vegetation typically displays a pattern of zonation in bands from land to sea as elevation changes. In northern New South Wales, mangroves border the lowest elevations with saltmarsh on slightly higher land. The saltmarsh of northern New South Wales is often dominated by three species, *Juncus kraussii* subsp. *australiensis* (Buchenau) Snogerup, *Sporobolus virginicus* (L.) Kunth and *Sarcocornia quinqueflora* (Bung ex-Ung. Sternb.) A.J. Scott subsp *quinqueflora*. The study locations were stratified to include sites where these dominant plant species were all present. Plant species were identified from Harden (1993; 2000) and confirmed by Dr Surrey Jacobs and Karen Wilson, National Herbarium, Royal Botanic Gardens, Sydney, Australia. All nomenclature follows PLANTNET, the electronic version of data from the Flora of New South Wales series, published by the UNSW Press, updated and maintained by the National Herbarium of New South Wales.

A quadrat (100 m x 10 m) was positioned across the saltmarsh to include the three major vegetation species. The northern edge of this quadrat was 50 m from the mangrove band bordering the saltmarsh. Within the 100 m x 10 quadrat, a central starting point for each survey was chosen using random numbers and a grid pattern. From each randomly selected central starting point, 4 x 5 m transects on each cardinal point provided a cross-pattern survey design to measure the gastropod densities with changes in vegetation in all directions from the centralised point (Figure 1). The survey design was adapted from studies in saltmarsh and freshwater wetlands of the mid north coast of New South Wales as described in Graham and Duggin (2000). This survey design was chosen to measure any changes in gastropod density with microtography. The survey design was repeated 3 times at Brunswick Heads. Along each of the 5 m directional transects, a contiguous series of 33 x 33cm quadrats (15 per 5 m transect) were set up. All gastropods were collected from the saltmarsh surface and counted from each quadrat, then returned to the quadrat, following the methods tested by Kaly (1988) and Breitfuss (2003). Only live snails on the surface were counted. An additional survey at Fingal Peninsula using the same design provided information to confirm findings across locations. A total of 180 (33 x 33cm) quadrats at Brunswick Heads and 60 quadrats at Fingal Peninsula were measured, a total of 240 survey quadrats over the two locations. The vegetation at the two locations was composed of the same plant species. Gastropods in each quadrat were counted on the falling tide, commencing one hour after the predicted tidal peak. One cross pattern survey was completed each day over a consecutive four-day period of king tides in January 2006. Gastropod densities and position in the marsh were recorded at a time when the majority were actively feeding.

Water depth was measured at the peak of the high tide, on the day of sampling each survey quadrat, to provide an estimate of the variation in elevation. Pieces of wooden dowel placed in the ground at each 33cm interval provided a measure of water level for each quadrat, transect and replicate. On the same day as the snail survey but during low tide, the height of the dominant vegetation, percentage cover of each plant species and distance to the nearest clumps of the tallest rush, *J. kraussii*, were measured in each of the previously sampled 33cm x 33cm quadrats. Vegetation cover for each species was determined by the subjectively estimation of the percentage area of each quadrat ($33cm^2$) covered by the foliage or bare soil in 10 classes between 0 and100. The percentage area covered by each species or bare soil was later grouped into four categories; 0-20, 21-40, 41-60, 61-100 for comparison of the results. The height of the foliage was measured from the ground to the top of the plant and grouped into three categories <10cm, 11-30cm, 31-90cm. Bare soil percentage was estimated from the visible area not covered by vegetation. Bare soil represented areas in the saltmarsh where an algal film may be present on the surface (Green, unpublished).

Identification of gastropod species in northern New South Wales saltmarshes.

Recent research has provided much-needed information about the taxonomy and distribution of the Australian Amphibolidae (Golding *et al.*, 2007). This taxonomic review concluded that the taxon previously known as *Salinator solida* (Woolcott 1945) was indeed a distinct species, *Phallomedusa solida* (Martens, 1878) and is now part of a new genus, *Phallomedusa* Golding *et al*, 2007. This species lives along the east coast of Australia in the supra-littoral zone and on soft mud in saltmarsh (Smith and Kershaw 1979; Golding *et al.*, 2007).

Recent reviews of the saltmarsh gastropods, *Ophicardelus* (Pulmonata, Ellobiidae) (Hyman *et al.*, 2004; *et al.*, 2005) distinguished three species, *Ophicardelus ornatus* Férussac, *O. sulcatus* H and A Adams and *Pleuroloba quoyi* H and A Adams. *Ophicardelus* spp. and *P. quoyi* occur along the east coast of Australia between the neap high tide level and the spring high tide levels in saltmarsh (Smith and Kershaw 1979; Hyman *et al.*, 2005.). The average shell length (7-12 mm) is similar for all species but *O. ornatus* is taller and more slender (Hyman *et al*,. 2004). Other species in east coast saltmarsh include *Cryptassiminea tasmanica* (Tenison Woods, 1876), previously known as *Hydrococcus tasmanica*) as reviewed by Fukuda and Ponder (2005), *Littoraria scabra*

(Linnaeus, 1758), *Melosidula zonata* (H and A Adams 1855) and *Tatea rufilabris* (Adams 1862) (Kaly 1988).

Ophicardelus ornatus, *O. sulcatus* and the similar species, *Pleuroloba quoyi*, all potentially occur in the saltmarsh of northern New South Wales (Hyman *et al*., 2005). *Pleuroloba quoyi* is distinguished from *Ophicardelus* spp. by the presence of a pallial gland and a muscular vagina (Hyman *et al*., 2005). Although these characteristics require microscope examination and are not identifiable in the field, the shells are significantly different (Hyman *et al*., 2004). *Ophicardelus ornatus* is distinguished by a taller conical shape and smooth surface without grooves. *Pleuroloba quoyi* has one groove above the suture and *O. sulcatus* has multiple grooves. Despite these known differences, the similarities between *O. ornatus* and *O. sulcatus* made absolute species determination difficult in the field, so *Ophicardelus* spp. was used to describe the colonisation and abundance of these two species in these saltmarsh field studies. Identification of *Phallomedusa solida* and *Littoraria scabra* was confirmed using Smith and Kershaw (1979) and Golding *et al.* (2007).

Data analyses

Relationships between the site factors (independent variables); tidal height, vegetation height, distance to *J. kraussii* (in 4 categories), percentage cover of vegetation or bare soil (0-100%) were tested against individual gastropod species densities (dependent variable) using a one-way analysis of variance (ANOVA). The differences between the means for distance from *J. kraussii* was investigated using Dunnets T3 post hoc multiple comparison test (equal variances not assumed) (SPSS 2001). For the analyses the skewness of data was assessed using graphical methods to determine any requirements for normalisation of data and reduction of variance heterogeneity (SPSS 2001). The gastropod data; densities of *Phallomedusa solida* and *Ophicardelus* spp, and the vegetation data; the percentage cover of *Juncus kraussii* and *Sporobolus virginicus*, were normalised using natural logarithms.

RESULTS

Dominant gastropod species in northern New South Wales saltmarsh

The pulmonate gastropods, *Phallomedusa solida* and *Ophicardelus* spp. dominated the saltmarsh at Fingal Peninsula and Brunswick Heads (Figure 2). *Ophicardelus* was the most commonly encountered genus in most samples (81.9%). Microscope examination in the laboratory confirmed *Ophicardelus ornatus* Férussac as the most common gastropod species at Fingal and Brunswick Heads, although *O. sulcatus* and *Pleuroloba quoyi* were present in some samples.

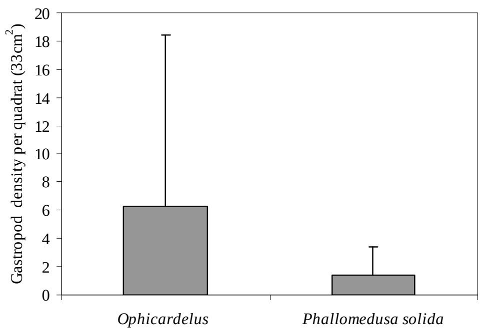

Figure 2: Mean and standard deviation of the major gastropod species(density per quadrat 33cm ^{2}) in saltmarsh at sites in Brunswick Heads and Fingal Peninsula, northern New South Wales (N=240).

Habitat associations of the pulmonate gastropods, *Ophicardelus* spp. and *Phallomedusa solida* in saltmarsh. The major plant species in the saltmarsh of the two northern New South Wales locations were *Sporobolus virginicus, Sarcocornia quinqueflora* and *Juncus kraussii. Sporobolus virginicus* was in the lower elevations but dominated the middle elevations providing the highest percentage cover in quadrats at both locations. *Sporobolus virginicus* was recorded in 82% of the survey quadrats at Brunswick Heads and 92% at Fingal Peninsula. The average height of *S. virginicus* was 22.5cm.

Sarcocornia quinqueflora is a succulent perennial herb that dominated the lower elevations, closer to the mangroves. The average height of *S. quinqueflora* in this study was 12cm, occasionally reaching >20cm in height but spreading over 30cm across the saltmarsh surface. *Sarcocornia quinqueflora* was recorded in 72% of the survey quadrats at Brunswick Heads and 15 % at Fingal Peninsula.

Juncus kraussii was recorded in 24% of the survey quadrats and 43% of quadrats at Fingal Peninsula. *Juncus kraussii* was the tallest species, forming clumps in the highest elevations of the saltmarsh but also in smaller clumps at lower elevations. The average height of *J. kraussii* at both locations was 65cm. Other taller plant species at both locations included *Baumea juncea* (45cm) and *Fimbristylis dichotoma* (50cm). The latter two species were not common in the survey quadrats (<10% cover) and no gastropods were recorded near these species. As the plant species in the survey quadrats and the percentage frequency of the major species were similar, the data from both locations were combined for analyses.

Qualitative observations after the tide had receded showed that, if not actively feeding on non-inundated surfaces, *Ophicardelus* spp. was in the leaf litter or inside clumps of *J. kraussii* while *Phallomedusa solida* was often feeding on the wet substrate or buried just under the wet surface. The test of densities of *Ophicardelus* spp. and *P. solida* with site variables revealed differences in habitat associations of the two gastropods. Densities of *Ophicardelus* spp. were significantly greater ($P<0.001$, $F= 0.803$, $Df =27, 180$) where the vegetation was higher (Table 1). Densities of *Ophicardelus* spp. were also higher with increasing percentage cover of *J. kraussii* and with up to 60% cover of *S. virginicus* (Figure 3). Densities of *Ophicardelus* spp. were lower at the highest percentage cover of *S. virginicus*. *Ophicardelus* spp. indicated an association with clumps of *J. kraussii.* Densities of *Ophicardelus* spp. were highest within 33cm of the clumps ($p<0.001$, Dunnets post hoc test). In contrast, densities of *P. solida* did not vary significantly with measured distances from clumps of *J. kraussii* (Figure 4). Percentage cover of the three dominant plant species, *S. quinqueflora, S. virginicus* and *J. kraussii*, with *Phallomedusa solida* were not significant (Table 1).

Elevation, measured as tidal height, was not significantly related to the densities of either *Phallomedusa solida* or *Ophicardelus* spp. The spp. were in quadrats with a lower percentage of bare soil (Figure 5). *Phallomedusa solida* was more evenly distributed in comparison to the percentage cover of bare soil (Figure 5). Vegetation height was not measured; variation in the tidal depth

Table 1:Gastropod densities tested against site habitat features; percentage cover (0-100%) of the three dominant plant species, percentage cover (0-100%) of bare soil, tidal height (measured as tidal depth), height of the dominant vegetation (cm), and densities of each gastropod species in relation to distance from *Juncus kraussii*, (4 categories) using ANOVA (SPSS 2001).

HABITAT FEATURE	***Phallomedusa solida***				***Ophicardelus spp.***			
Percentage cover	P	F	Df	MS	P	F	Df	MS
Sarcocornia quinqueflora (Bunge ex Ung. -Sternb.) A.J. Scott subsp. *Quinqueflora*	0.723	0.777	18, 119	0.385, 0.495	0.093	1.500	18, 189	1.884, 1.256
Sporobolus virginicus (L.) Kunth.	0.576	0.912	21, 116	0.445, 0.487	< 0.0001	3.258	21, 186	3.474, 1.066
Juncus kraussii Hochst. subsp. *australiensis* (Buchenau) Snogerup	0.100	1.599	12, 125	0.731, 0.457	< 0.0001	11.089	13, 194	8.897, 0.802
Bare soil	0.004	2.207	22, 115	0.889, 0.403	< 0.0001	4.91	23, 184	4.489, 0.913
Distance from *Juncus kraussii* (4 categories)	0.811	0.396	4, 133	0.194, 0.490	< 0.0001	24.777	4, 203	22.251, 0.898
< 33cm from *Juncus kraussii* (Dunnets T3 post hoc)					< 0.001			
Tidal height (cm)/ elevation	0.819	0.747	30, 107	0.380, 0.590	0.099	1.367	35, 172	1.687, 1.234
Height of vegetation (cm)	0.487	0.986	22, 115	0.475, 0.482	< 0.001	10.803	27, 180	6.214, 0.575

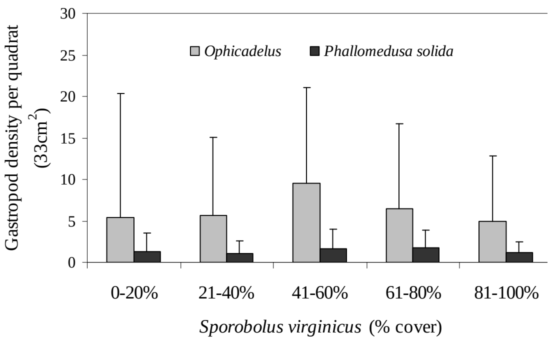

Figure 3: Mean density (+- SD) of dominant gastropod snails in saltmarsh at sites in Brunswick Heads and Fingal Peninsula, northern New South Wales (N=240) in five categories of increasing cover of *Sporobolus virginicus.*

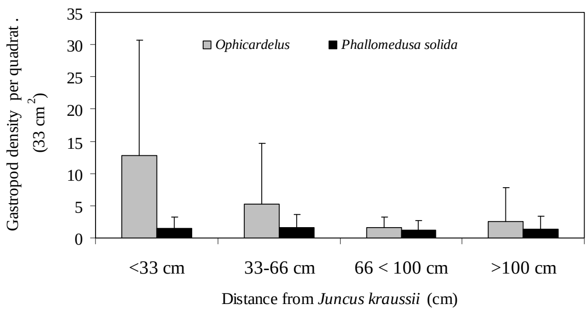

Figure 4: Mean density (+- SD) of dominant gastropod snails in saltmarsh at sites in Brunswick Heads and Fingal Peninsula, northern New South Wales (N=240) in four categories of distance from *Juncus kraussii*. Association of *Ophicardelus* spp. with *Juncus kraussii* is evident by the decreasing number of snails with increasing distance from the clumps of *J. kraussii*. In contrast, the density of *Phallomedusa solida* does not change with distance to *J. kraussii*.

was 19.5cm across the study sites. Higher numbers of *Ophicardelus* a significant factor in relation to the density of *P. solida* but greater densities of *Ophicardelus* spp. were in the taller vegetation (Figure 6). *Juncus kraussii* was the tallest species in the survey sites.

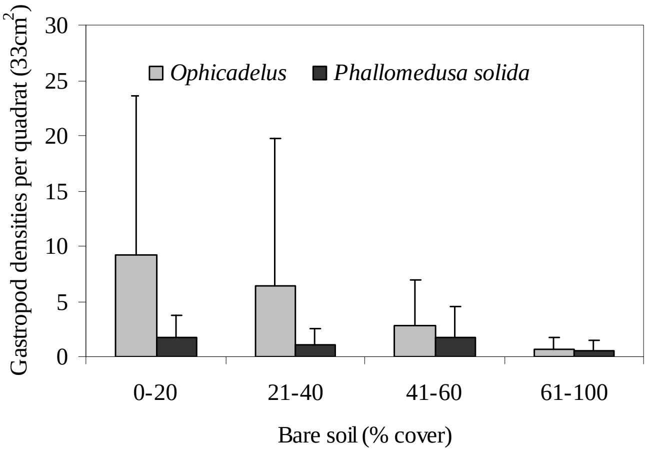

Figure 5: Mean of gastropod density per quadrat with increasing cover of bare soil (less vegetation cover) in four percentage cover categories (error bars are standard deviation) in saltmarsh at sites in Brunswick Heads and Fingal Peninsula, northern New South Wales (N=240). Bare soil also represented areas where an algal film may be present. The association of Ophicardelus spp. with higher vegetation cover is evident by the higher density of snails with lower bare soil percentages. In contrast, the density of *Phallomedusa solida* is more evenly distributed.

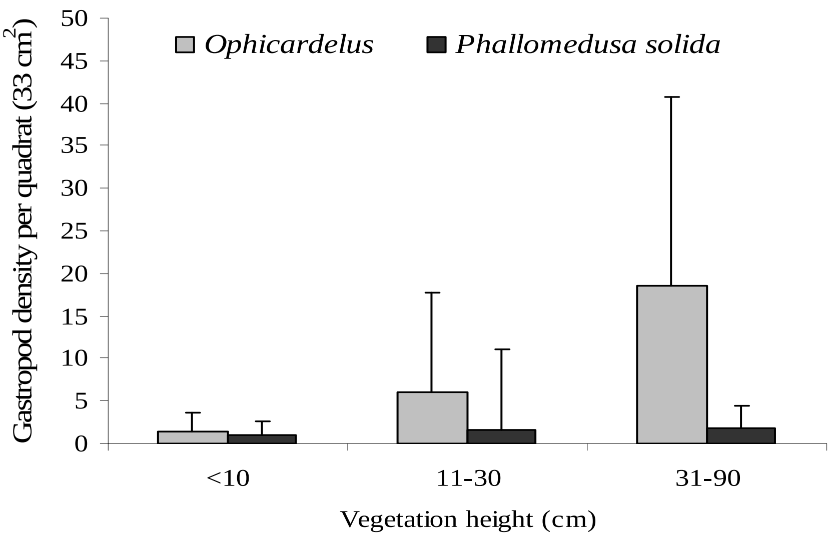

Figure 6: Mean of gastropod density per quadrat (N=240) compared to increasing vegetation height in three size categories (error bars are standard deviation) in saltmarsh at sites in Brunswick Heads and Fingal Peninsula, northern New South Wales (N=240). The habitat associations of Ophicardelus spp. are evident by the higher density of snails in the quadrats with taller vegetation. In contrast, the density of *Phallomedusa solida* is more evenly distributed in relation to vegetation height.

DISCUSSION

Ophicardelus spp. have been reported from saltmarsh in nearby south-east Queensland, including at slightly higher elevations next to mangroves (Morgan and Hailstone 1986) and also at even higher elevations in *Casuarina* forest (Shine, Ellway and Hegerl 1973) so it was not unexpected to find these gastropods in high densities in similar habitat at the relatively close locations of Brunswick Heads and Fingal Peninsula. Elevation will influence the establishment of the individual saltmarsh plant species (Hutchings and Saenger 1987; Adam 1990). The structure that these plants provide as habitat will influence dispersal and recruitment into new habitats (Armitage and Fong 2004). Elevation was not a significant factor in the densities of gastropods within the narrow topographic range of this study, but elevation has been a factor influencing gastropod densities in other studies (Morgan and Hailstone 1986, Breitfuss 2003). This may be due to the available plant species and the habitat structure that they provide. It may be expected that differences in gastropod densities would be significant across a greater elevation gradient with more pronounced differences in habitat structures.

Hot or dry and windy weather conditions appeared to reduce numbers of gastropods actively feeding on the bare saltmarsh. In contrast, cloudy or light rain appeared to increase numbers of gastropods actively feeding. At high tide, *Ophicardelus* spp. were predominately found climbing on the stems of *J. kraussii* above the tide level, but were not in *Baumea juncea* or *Fimbristylis dichotoma. Phallomedusa solida* was not on the stems of any saltmarsh plants at high tide. *Ophicardelus* spp. were also in litter at higher elevations, just beyond the tidal limit and in terrestrial environments near *Casuarina glauca* at Fingal and Brunswick Heads. An increase in numbers of *Ophicardelus* spp. and *P. solida* with an increase in tree litter was identified in a study of these species in mangrove microhabitats of Sydney Harbour (Michie 2001).

This study has demonstrated that *Ophicardelus* spp. have a habitat association with tall vegetation, particularly for *J. kraussii* and taller *S. virginicus*. The air-breathing *Ophicardelus* spp. needs to escape from higher tides and subsequent predation by fish but also needs shelter from desiccating conditions on the saltmarsh surface at low tide. Tall dense stands of *S. virginicus* may offer this cover at lower tidal levels (<22.5cm deep) but *J. kraussii* forms thick clumps offering maximum protection from desiccation (and possibly predation by birds) at the base under dry conditions and on the stems at highest tides. The taller sedges, *Baumea juncea* and *Fimbristylis dichotoma*, also present in the same tidal zones in northern New South Wales, have thinner and weaker stems (1-2 mm wide) than the widespread *J. kraussii* (1.8-4.5 mm wide) so may not provide the same structural strength for tidal escape by *Ophicardelus* spp. In a study of Tasmanian saltmarsh gastropods (Richardson *et al.*, 1998), high numbers of *O. ornatus* were in quadrats near *Gahnia filum* (Labill.) F. Muell., a strong-stemmed dense sedge growing to 100cm tall with stems 2-3 mm wide, and *Sclerostegia arbuscula* (R.Br.) Paul G. Wilson, a perennial chenopod growing to 2 m tall with stems to 5 mm in diameter. The high numbers of *O. ornatus* in these saltmarsh plants appears to confirm the association with taller and strong-stemmed vegetation. At low tide, the dense and taller vegetation offers protection from desiccation for *Ophicardelus* spp. Other studies have demonstrated that *Ophicardelus* spp. are often in the cover of vegetation (Kaly 1988, Richardson *et al.*, 1998). In an experimental study of saltmarsh gastropods in Sydney, New South Wales, *Ophicardelus* spp. colonised plots with 100% cover of *Sarcocornia quinqueflora* rather than plots with only 50 % cover (Kaly 1988).

In the study of Tasmanian saltmarsh gastropods, *Ophicardelus ornatus* Férussac, reached high densities where *J. kraussii* was present (Richardson *et al.*, 1998). The Tasmanian saltmarsh had a greater diversity of taller species than the New South Wales saltmarsh. However, other recent studies have shown that *Ophicardelus* spp. are commonly associated with the shoots of *Sporobolus virginicus* and *J. kraussii* at other locations along the New South Wales coast (Ross *et al.*, 2009). McGuiness (1994) showed that the climbing behaviour demonstrated by the gastropod, *Cerithidea anticipata* in mangroves in northern Australia was more common at low tide for shelter and to prevent desiccation, rather than to escape from the high tide as originally thought. The climbing behaviour of *Ophicardelus* spp. and the apparent association with taller vegetation has not been studied but predation may be a factor as well as the need to breathe.

In contrast to the other studies, Roach *et al.* (1989) reported a pattern of distribution of *Ophicardelus* spp. that was predominantly at the lower elevations towards mangroves but Roach *et al.* (1989) also noted an exception to this distribution pattern was on more elevated sites where *J. kraussii* grew and high numbers of *Ophicardelus* spp. were present. The apparent distribution of *Ophicardelus* spp. at lower elevations may occur in periods of lower tidal cycles. The importance of accounting for changes in abundance of gastropods over different temporal scales was noted in a study of saltmarsh gastropods (Wong 2002).

It has been reported that the lower sites near mangroves offered a stable temperature and moisture microhabitat for gastropods (Roach *et al*,, 1989), but there is evidence from this study that *Ophicardelus* spp. occur in the protection and the humid environment offered by taller strong-stemmed vegetation, particularly *J. kraussii* in northern New South Wales.

P. solida had different habitat associations to *Ophicardelus* spp. *P. solida* was more evenly distributed across the saltmarsh. Kaly (1998) found *P. solida* was negatively correlated with increasing percentage cover of *S. quinqueflora*, and was common on bare soil. Wong (2002) also recorded that there were greater abundances of *P. solida* in patches of bare sediment, than in saltmarsh vegetation. Roach *et al.*, (1989) reported that densities of *P. solida* did not vary between the bare substrate down-shore mangrove sites and the up-shore saltmarsh sites. In a saltmarsh study in southeast Queensland by Breitfuss (2003) elevation was a significant factor influencing the distribution of both *P. solida* and *Ophicardelus* spp. The highest densities of both gastropods were at 30 m and 50 m from the mangroves (or mean low water).

Although habitat features affect the overall distribution, abundance and size of gastropods (Kaly 1988), the physical and structural features of the individual species may influence habitat niche selection and assist in survival in the extreme conditions of the saltmarsh environment (Armitage and Fong 2004, R.E. Golding, unpublished data, 2007).

The operculum is a calcareous structure on the dorsal side of the gastropod tail that closes off the external opening of the shell when the animal withdraws inside (Smith and Kershaw 1979), appearing to prevent desiccation in dry conditions or deter predators. The Amphibolidae is the only pulmonate or air-breathing family with an operculum (Smith and Kershaw 1979). The operculum relates to the primitive phylogeny of *P. solida* and the Amphibolidae (Golding *et al.,* 2007) and is not considered an adaptation to their current environment although it may assist in their survival (R.E. Golding, unpublished data, 2007). The operculum in *P. solida* is a major structural difference from *Ophicardelus* spp. and may be one reason for the different habitat requirements of these gastropods.

The ciliated strip in the mantle cavity of *P. solida* and other amphiboloids has been suggested as a more likely reason for their distribution in saltmarsh because it allows water to circulate and suggests a mechanism for survival, if not a requirement to live in shallow water and muddy substrates (R.E.Golding, unpublished data, 2007; Golding *et al.,* 2007). This morphological feature may be a reason for their apparent preference for the less vegetated, more frequently inundated surfaces, where it is easier to burrow into the substrate (Kaly 1988). Although the family of *Ophicardelus* spp, the Ellobiidae, is also primitive, the operculum has been lost and *Ophicardelus* spp. have become 'terrestrial'. This is confirmed by its association with taller vegetation in this study and higher micro elevations in the saltmarsh (Breitfuss 2003). The protection offered by the density of *J. kraussii* appears to offer shelter to *Ophicardelus* spp species from desiccation.

The design of restoration projects may need to account for these species associations to provide habitat for the range of fauna in saltmarsh. The saltmarsh gastropods are known to burrow into the mud making accurate counting of numbers more difficult (Ross *et al.,* 2009). It is essential that the design of monitoring and assessment programs of fauna abundances account for the individual species associations, as indicated by the example of *Ophicardelus* spp. in this study.

The failure to find high densities of a common gastropod species such as *Ophicardelus* spp. may indicate that the habitat is unavailable or the species may be sheltering in tall dense vegetation to avoid desiccation or higher tides. Additionally, the associations of the different species with specific habitat features may vary over a latitudinal gradient. To gauge the success (or not) of restoration projects by gastropods densities alone would be in error if habitat features were not considered.

CONCLUSION

This study confirms the hypothesis that the pulmonate gastropods, *Ophicardelus* spp. are more frequently found in taller vegetation in saltmarsh and have different habitat requirements to other common saltmarsh gastropods such as *P. solida*. Although the microhabitat of gastropods in saltmarsh of the New South Wales coast overlaps, the associations of the individual species are different.

Ophicardelus spp. requires the shelter and strength of taller vegetation or some passage to escape tidal water in the saltmarsh. *P. solida* is commonly associated with mud substrates and does not need to climb on vegetation at high tide. It is apparent that if the preferred habitat for the species is not present it is unlikely that densities will be high. Understanding and incorporation of fauna habitat associations is extremely relevant in restoration project design to cater for the targeted species.

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