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Response of Salt Marsh to Anthropogenic Disturbance: Effects of Removal of Surface Vegetation on Structure and Function



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SUMMARY

A manipulative experiment was conducted in southern Moreton Bay, Queensland, to investigate the response of *Sporobolus virginicus* salt marshes to disturbance in the form of removal of surface vegetation. Replicated control and treatment plots of 5, 10 and 20m diameter were set up on Cobby Cobby Island and Eden Island in October 2001. Removal of surface vegetation was effected by mowing in the treatment plots in early November, and the macroinvertebrate assemblages were monitored over an 18-month period after the disturbance. The plots were designed to allow tests of the effect of plot size and position in plot on the response of the macroinvertebrate assemblages. Three groups of macroinvertebrates were sampled, namely, the macrobenthos, the mobile epibenthos, and juvenile nekton and plankton. The macrobenthos were sampled using a hand held corer and sieved over a 125 μ m mesh. Mobile epibenthos, mainly grapsid crabs, were sampled using pitfall traps, while juvenile nekton and plankton were monitored using 'simulated aquatic microhabitats' (SAM). The aboveground biomass of *S. virginicus* was measured by harvesting all aboveground vegetation during the preparation of the experimental plots. Nutrient and organic matter availability in the experimental plots were measured by the concentration and the stable isotope signatures of carbon and nitrogen in the sediment. Possible changes in the trophic base of the experimental plots were studied by the stable isotope signature of a dominant consumer, the grapsid crab *Helograpsus haswellianus*.

A total of 100 morphospecies were recorded for the three macroinvertebrate groups. The *Sporobolus* marshes support a macrobenthos assemblage with species richness (46) similar to other marshes including the well-studied Atlantic marshes, but at significantly lower levels of abundances. Aboveground biomass of *Sporobolus*

virginicus averaged at 302.8 g dry wt m⁻², the low value reflecting the small stature of this species compared to the Atlantic *Spartina* spp. While this growth form may influence the response of *S. virginicus* to disturbance, the experiment suggests that removal of surface vegetation has negligible long-term impact on the structure and function of the salt marsh. Eleven and 85 morphospecies were recorded, respectively, for the mobile epibenthos and SAM samples. Despite common significant temporal differences in assemblage structure and abundance, none of the three faunal groups demonstrated significant differences between the control and experimental plots, as suggested by univariate analyses of species diversity and richness, abundance, and evenness. Multivariate analyses of assemblage structure and composition using analysis of similarity (ANOSIM) and multidimensional scaling (MDS) techniques also failed to detect significant differences due to treatment for the three faunal groups. Patterns of carbon and nitrogen content of the sediment and *H. haswellianus* suggest a weak trend of decreased nutrient availability and condition of the crab in the treatment plots. In both treatment and control plots, however, *S. virginicus* remained to be the dominant source of organic matter in the sediment, which was utilized by *H. haswellianus* as the major food item irrespective of the treatment. Unlike mangroves, which are known to be strongly affected by removal of surface vegetation, *S. virginicus* salt marshes are probably highly resilient to such disturbances. This resilience of local salt marsh to surface disturbance probably plays a role in maintaining coastal wetland landscapes on human influenced coasts.

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1. INTRODUCTION

1.1 Salt marsh functional ecology

Research interests in salt marsh systems ecology dates back to the 1950's, with the main thrust occurring on the Atlantic coast of North America. This is not surprising as extensive marshes dominated by the smooth cordgrass *Spartina alterniflora* flourish along those coasts, forming an important feature of the coastal landscape. In contrast to the relatively dwarf Australian salt marsh species, *S. alterniflora* grows to about 2m tall under favourable conditions, providing significant habitat complexity to estuarine biota and shelter from unfavourable abiotic conditions. Papers presented at the Salt Marsh Conference held on Sapelo Island at the University of Georgia Marine Institute (UGAMI) represent one of the earliest efforts in integrating salt marsh systems ecology from the perspectives of geology, hydrography, nutrient dynamics and ecology (Ragotskie et al. 1959). At the same conference, one of the most important papers in salt marsh systems ecology was presented by Teal (1959), which started the focus of salt marsh systems ecology on their ability to support nearshore secondary production in the following 50 years. Later termed "outwelling" by Eugene Odum (Odum 1968), the question of how salt marshes support nearshore fishery production has attracted immense research efforts, with many models proposed to depict the trophic and non-trophic inter-connection between different habitats in temperate estuaries (e.g. Odum 1968, Nixon 1980, Dame & Allen 1996, Kneib 1997a).

Various measurement approaches have been used in the attempt to elucidate the trophic importance of salt marshes to estuarine production, including nutrient and organic matter flux measurements (Wolaver et al. 1985, Childers & Day 1988) and employment of chemical tracers (e.g. Haines 1977, Gearing 1988, Weinstein et al. 2000). The advance of these techniques have established that north Atlantic salt

marshes are generally highly productive (up to $>3500 \text{ g dry mass m}^{-2} \text{ y}^{-1}$ aboveground primary production), with productivity in a broad scale generally regulated by latitude and tidal amplitude (Day et al. 1989). The trophic contribution of salt marsh to coastal production is, however, more controversial, with significant variations in different systems, probably dependent on attributes such as the age of the estuary and local hydrological conditions (Odum et al. 1979, Nixon 1980, Dame et al. 1992). Recent studies have also shown that previously neglected sources of primary production, such as benthic microalgae, could provide more directly utilisable carbon to estuarine consumers in comparison to vascular plant detritus (Sullivan & Montcreiff 1990, Mallin et al. 1992).

Recent research also confirms that Atlantic salt marshes act as important habitat for the nekton, not only for transient but also resident species. Kneib (1997a) argued, based on the life history characteristics of estuarine nekton and the landscape features of intertidal salt marsh ecosystems, that many resident nekton species perform a “trophic relay” in transferring organic production from the salt marsh into the estuary. Large, transient consumers such as predatory portunid crabs (e.g. *Callinectes sapidus*) and fish are known to frequent intertidal salt marshes during the high tide (e.g. Rozas & Hackney 1984, Ryer 1987, Kneib 1991, Connolly et al. 1997, Thomas & Connolly 2000, Paterson & Whitfield 2003). The three-dimensional habitat fabric provided by *Spartina alterniflora* and the other Atlantic salt marsh plants significantly modifies predator-prey interactions (e.g. Minello & Zimmerman 1983, Lee & Kneib 1994), also providing physical refuge from environmental stresses such as desiccation (e.g. Kneib 1994).

1.2 Salt marshes of Australia

Salt marshes occur extensively throughout the Australian coastline, demonstrating an inverse pattern in species richness compared to the mangroves (Hutchings & Saenger 1987). Occurrence extends to not only the temperate but also tropical and sub-tropical areas, although species richness is relatively low (<10) in tropical regions compared to the highly diverse (>50 species) assemblages in southern Australia (Saenger et al. 1977). The most extensive development of salt marshes occur on the North Coast and Gulf of Carpentaria bioregions, accounting for ~8600 and ~3800 km² respectively (Department of Environment, Sport and Territories 1996).

Australian salt marshes are physiognomically distinct from their counterparts in the north Atlantic, thus questioning the applicability of most of the current paradigms in salt marsh ecology, which have largely originated from the Atlantic systems. The dominant salt marsh plant in sub-tropical Southeast Queensland, *Sporobolus virginicus* (salt couch), for example, is a small species usually < 30cm tall. The shoots are only ~2 mm thick and the plant is generally much less robust than *Spartina* species (Figure 1).



Figure 1. *Sporobolus virginicus*, the dominant salt marsh plant species in Southeast Queensland. Height of the grass seems to be influenced by factors such as salinity and hydroperiod, but is usually <30 cm.

Other common Australian salt marsh species, e.g. *Sarcocornia quinqueflora*, *Saeuda australis* and *Sesuvium portulacastrum*, are low shrubs or herbs so the Australian salt marsh landscape is distinctly different from their much better known Atlantic counterparts (Figure 2).

A brief survey of the number of papers on Australian salt marshes recorded in the *Aquatic Sciences and Fisheries Abstracts* (ASFA) between the years 1960-2004 returned only 96 entries, whereas the total number of papers on salt marshes is 3192 during the same period, i.e. Australian salt marsh studies only make up ~3% of the global research output in the last 44 years. Much is yet to be learned about Australian salt marshes.

1.3 Threats to Australian salt marshes

There is a dearth of information on the status and ecology of Australian salt marshes. It is clear, however, that salt marshes have suffered significant losses because of conversion into urban and industrial developments and their ancillary structures such as ports and marinas (Department of Environment, Sport and Territories 1996). In Southeast Queensland, one of the most important causes of loss has been conversion into canal residential developments. In Southeast Queensland alone, it has been estimated that >1200 ha of mangroves and almost 600 ha of salt marsh-claypan areas were lost between 1974 and 1987 (Hyland and Butler 1989). During the same period, the area of artificial waterways and canals increased to about 5% of the area of natural mangroves and salt marsh-claypans in the region.

Apart from direct habitat destruction, salt marsh habitats in Australia are also subjected to many other threats, including discharge of nutrients and grazing. Grazing is a common process affecting European salt marsh systems (Adam 1990).



Figure 2. Differences between the physiognomy of sub-tropical Australian salt marsh in Southeast Queensland (A) and a typical marsh dominated by *Spartina alterniflora* on Sapelo Island, Georgia, USA (B). Note the much taller grass in the Atlantic marsh.

Saintilan & Wilton (2001) reported a significant intrusion by mangroves into temperate Australian salt marshes. It is unclear what exactly caused this shift in balance, but the change is likely to be related to local processes such as changes in the sedimentation-erosion regime, and global phenomena such as sea level rise and temperature increase.

1.4 Aims of this study

This study aims to investigate the response of sub-tropical Australian salt marsh habitats to anthropogenic disturbance. A concurrent study carried out on the salt marshes of Sapelo Island, Georgia, USA, in conjunction with Dr Ron Kneib of the University of Georgia, attempts to compare the response of Australian and Atlantic salt marshes when applied with the same disturbance. Results of the Atlantic experiment will be reported elsewhere and will not be discussed in this report. The disturbance applied was in the form of the removal of surface vegetation by mowing. As salt marshes are generally protected from large scale disturbance by law in Queensland, this manipulation serves to simulate removal of surface biomass by disturbances such as grazing. Specifically, the manipulative experiment aimed at investigating the impact of this disturbance on

- Macroinvertebrate assemblage structure
- The availability and utilisation of salt marsh organic matter as food by resident macroinvertebrates

The influence of the scale of the disturbance (in terms of the area affected) was compared through treatment applied to plots of 3 different sizes. Plot size effects were also compared by monitoring response of the macroinvertebrate pattern at different distances into the disturbed area.

2. MATERIALS AND METHODS

2.1 Study locations

The manipulative experiment was conducted on salt marshes of Cobby Cobby Island (27.72°S 153.39°E) and Eden Island (27.75°S 153.39°E) in southern Moreton Bay, Queensland (Figure 3).

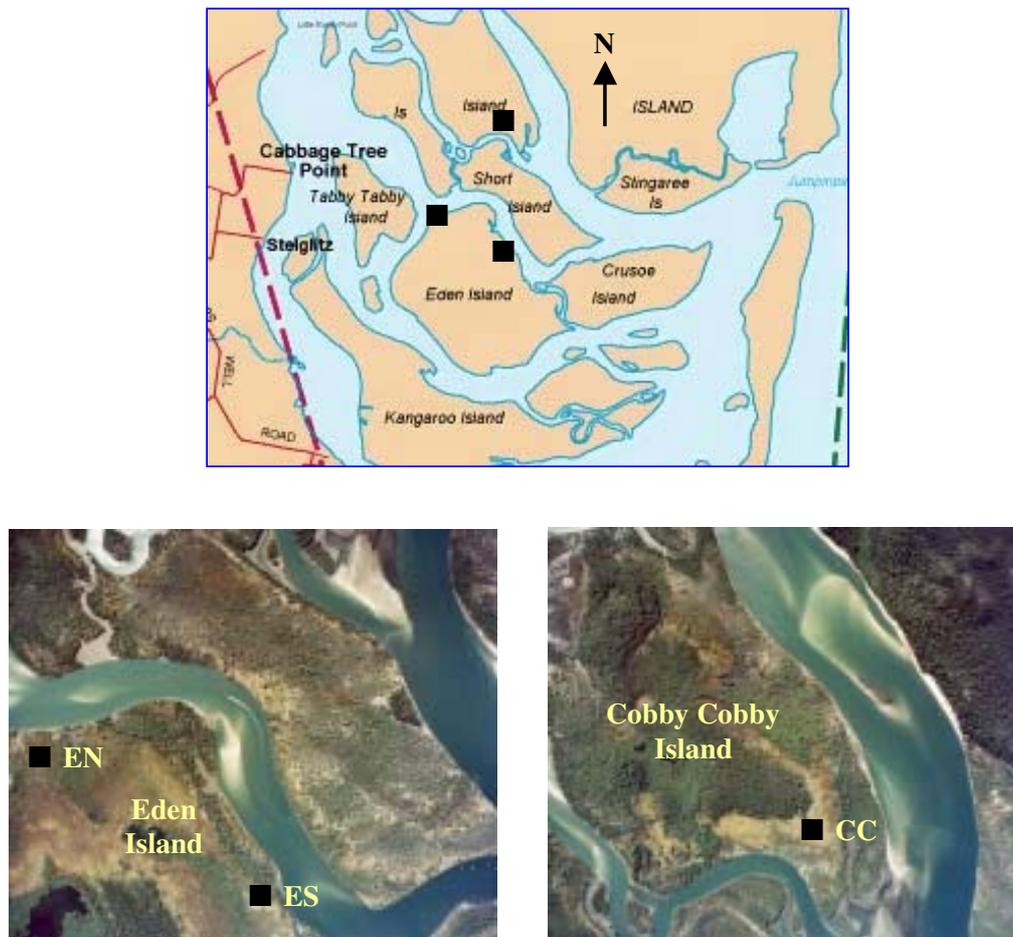


Figure 3. Map of southern Moreton Bay showing the location of the study plots on Cobby Cobby Island and Eden Island. The position of the manipulated plots are shown by “■” in the aerial photographs. The two locations on Eden Island are respectively labelled as Eden North (EN) and Eden South (ES).

Extensive salt marshes occur on these and other islands in southern Moreton Bay, part of the Moreton Bay Marine Park. The Marine Park offers protection to these salt marsh areas, as no disturbance may be made to salt marshes and other marine plant habitats without a permit from the Marine Park authority. The salt marsh habitats here are dominated by the salt couch *Sporobolus virginicus*, often fringed on the seaward side by mangroves dominated by *Avicennia marina*. Other salt marsh plant species include *Saeuda australis* and *Sarcocornia quinqueflora* but their abundances are generally low. *Sporobolus virginicus* in the experimental plots were generally <25 cm in height.

2.2 Experimental design

The manipulative experiment is conducted by applying a common disturbance, namely, removal of surface vegetation by mowing, to 3 replicated plots of 3 sizes. Each position marked in Figure 3 had one complete set of treatment plots comprising one circular plot each of, respectively, 5, 10 and 20 m diameter, and another set of control plots (no mowing) of the same sizes. Response of the plots to the applied disturbance was monitored over a 2-year period, with 6 sampling events (Figure 4). Removal of salt marsh vegetation occurred on 6 November 2001, while the first set of samples was collected three weeks prior to the disturbance, i.e. 17 October. Post-treatment samples were collected 6 weeks (Round 2; 18 December 2001), 16 weeks (Round 3; 26 February 2002), 33 weeks (Round 4; 24 June 2002), 52 weeks (Round 5; November 2002) and 82 weeks (Round 6; June 2003) after the initial disturbance. The areas of the plots were 19.63 (5m), 78.5 (10m) and 314m² (20m).

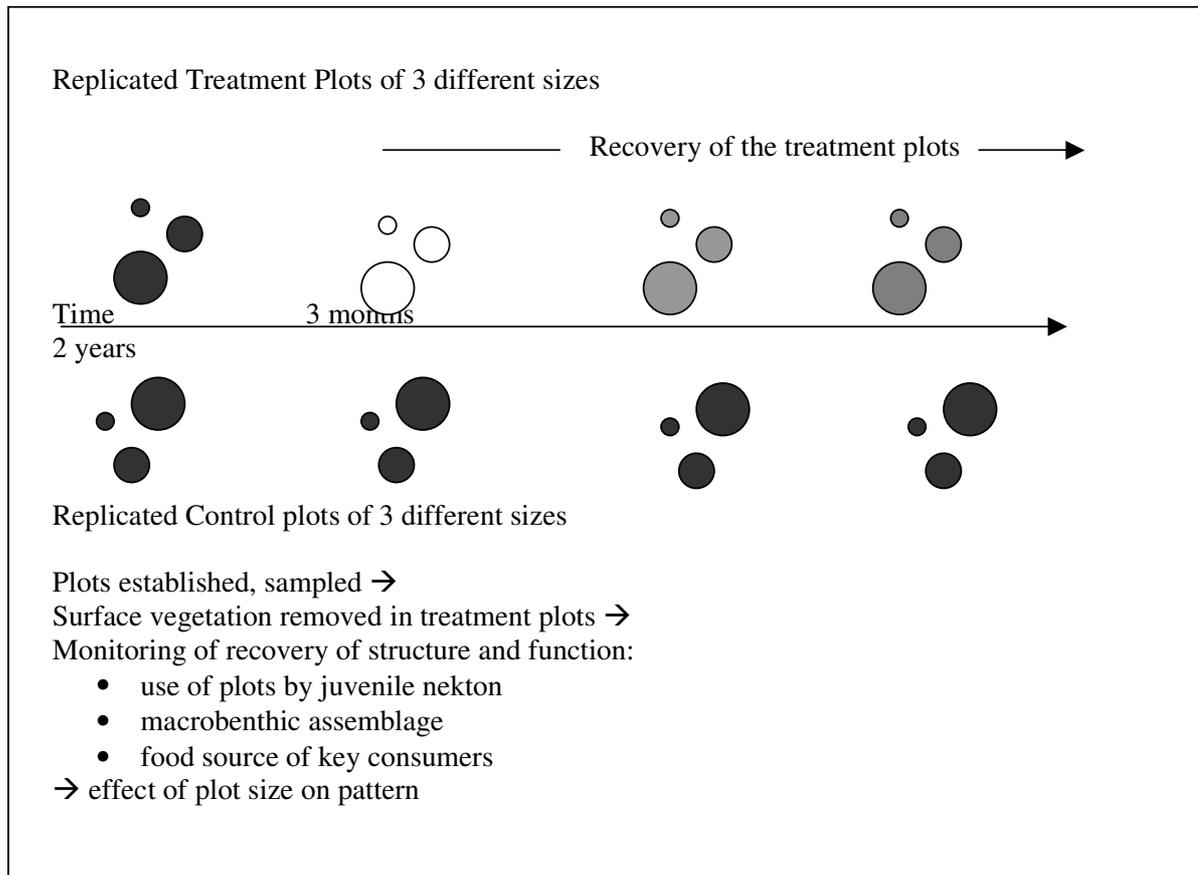


Figure 4. A schematic diagram of the experimental design.

In order to evaluate the influence of distance from the edge of the disturbance on the biotic assemblage, the circular plots were divided up into 3 concentric cores equidistant from the centre (Figure 5). To cater for possible effects of sampling disturbance on the plots, the same level of sampling intensity, i.e. the number of samples collected per unit area of the plots, was applied to plots of different sizes. This necessitates that only a sector of the larger (90° sector for 10m plots, 22.5° sector for 20m plots) plots was used for sampling, while the whole of the smallest plots (19.6m^2) would be used (Figure 6). The first sets of samples were collected on 22

October 2001, and the mowing treatment was applied to the plots on 6 November 2001.

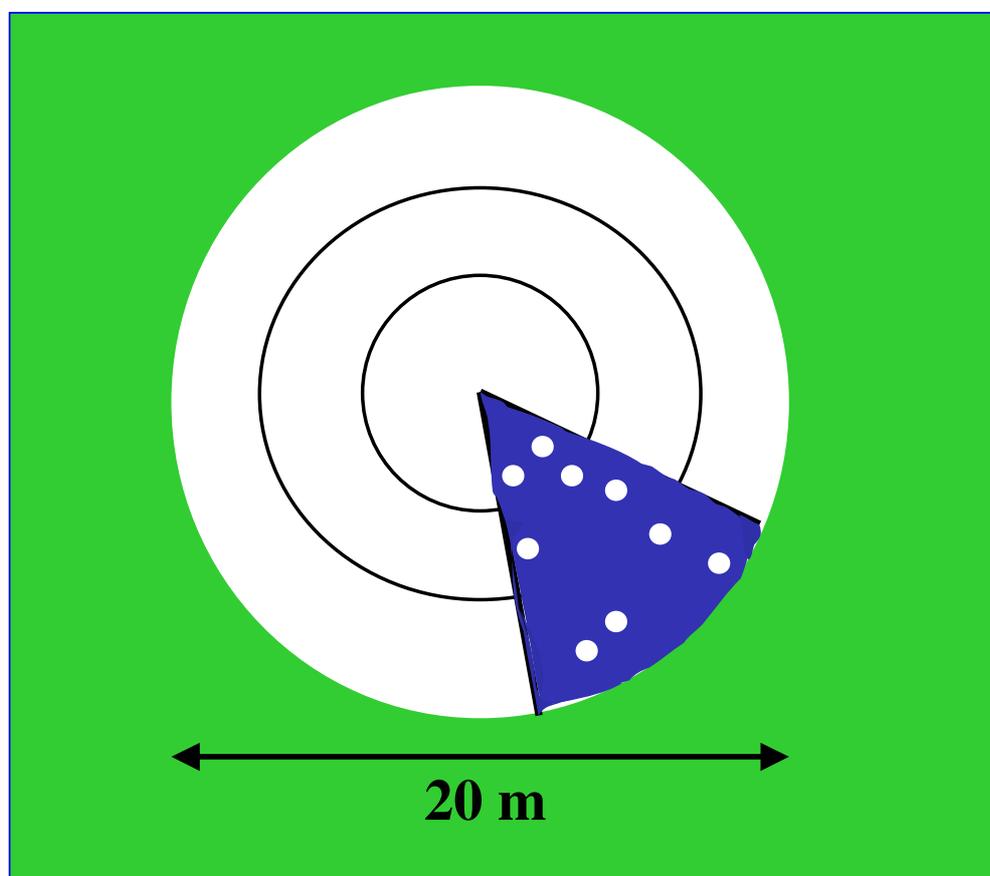


Figure 5. A schematic diagram illustrating the organisation of the 3 concentric cores and the sector used for sampling in a 20m-diameter plot. The 22.5° blue sector represents the same area as a 5m-diameter plot, i.e. 19.6m². The number of samples collected from the 3 concentric cores (2, 3, and 4) are standardised by their areas to give the same sampling intensity. The number of samples collected from the inner, middle and outer cores were, respectively, 3, 9 and 15, for each sector.



Figure 6. Part of a 20m-diameter treatment plot marked out on Eden Island in May 2002, 6 months after the initial disturbance. Note that the boundary of the plot (indicated by white arrows) was still clearly visible, despite significant regrowth of *Sporobolus virginicus*. Location of the concentric core boundaries are marked by the white PVC pipes.

2.3 Sampling

Sampling was conducted on 6 occasions over a 2-year period, with sampling occurring every 3 months in the first year and every 6 months in the second year. All sampling took place during the spring low tide period, when the salt marshes were expected to have been inundated by tides a few hours prior to the sampling. Because of the large number of samples to be collected, the 3 locations were visited on separate but consecutive days.

Division of the circular plots into 3 concentric cores resulted in 3.33m, 1.66 and 0.83m radius intervals for the plots of 5, 10 and 20m diameter, respectively. In order to standardise sampling intensity, i.e. to have the same number of samples collected per unit area of plot, the numbers of each type of samples (macrobenthos, SAM, and pitfall samples) were 3, 9 and 15 respectively for the inner, middle and outer cores.

2.3.1 Aboveground biomass of *Sporobolus virginicus*

The aboveground biomass of *Sporobolus virginicus*, the dominant vegetation on the salt marsh, was estimated before the start of the experiment to give an indication of the condition of the experimental plots, and how the standing crop biomass compares with documented values in other systems. Three randomly selected 1m² plots of *S. virginicus* were selected at each sampling location (n = 9) and the aboveground vegetation clipped by hand, bagged and weighed to give an estimate of the aboveground biomass of *S. virginicus*. The material was then dried at 80°C until constant weight to determine the dry biomass. The biomass collected was divided by the area to provide an estimate of standing crop biomass.

2.3.2 Macroinvertebrate assemblages

2.3.2.1 Juvenile nekton and plankton

The method for sampling juvenile nekton and plankton involved the use of “Simulated Aquatic Microhabitats” (SAMs, Kneib 1997b). These devices are simply 10cm diameter/7cm deep plastic takeaway containers, designed to capture both micro (e.g. copepods) and macroscopic species (juvenile fish). When the tide recedes, an artificial pool created by the container is left which serves to congregate small nekton

in them. Although not providing measurement of absolute juvenile nekton density, SAMs allow the relative abundance of juvenile nekton using the habitat to be compared amongst the study locations. The SAMs were placed flush with the sediment, and were left 24 h over 2 tidal cycles. Juvenile nekton retained by the SAMs were separated from the water in the laboratory using a 125 μ m sieve. There is usually a small amount of sediment that needs to be washed out of each SAM. All material remaining after sieving was placed into 120ml vials, containing ethanol for preservation. The species were sorted in the laboratory using a dissecting microscope, after staining with rose Bengal. A photographic catalogue has been constructed of all the species collected, along with drawings and detailed descriptions for identification. Identification was conducted to the lowest taxonomic level possible, but most of animals were, expectedly, small and often could only be identified to the family or higher levels. Focus was placed on comparing the overall structure of the assemblage between the experimental plots rather than on individual species.

2.3.2.2 Macrobenthos

Macrobenthos at the study plots were collected using a corer. Each core sample (15cm high by 10cm diameter) was taken using an aluminium corer at random locations within each plot, following the numbers described in section 2.3. The major taxa encountered were polychaete and oligochaete worms, crabs, and gastropods. Because of the relatively impoverished fauna, all core samples were sieved through a 125 μ m mesh, to wash out unwanted sediment, but to retain all macro- and large meiofauna. Sorting and identification was carried out using sorting trays on rose Bengal stained samples. Any animals visible to the naked eye were collected, usually > 5 mm in length.

2.3.2.3 Ground dwelling crabs and other mobile epibenthos

Pitfall traps were used in the trapping of crabs (and other mobile epibenthos), providing a measurement of relative crab activity in the salt marsh plots (Figure 7). Sections of 10 × 10cm PVC pipe was used with 2 mm fly mesh as a base, which prevented the crabs from escaping until the traps were collected. The pitfall traps were also left for 24 hrs and collected during the low tide of the following day. The same numbers of samples were taken for the pitfall traps as the SAM and core samples. Crabs were initially stored frozen until sorting and identification, but were identified on site and released later in the sampling program to minimize the effect of removal on the populations.

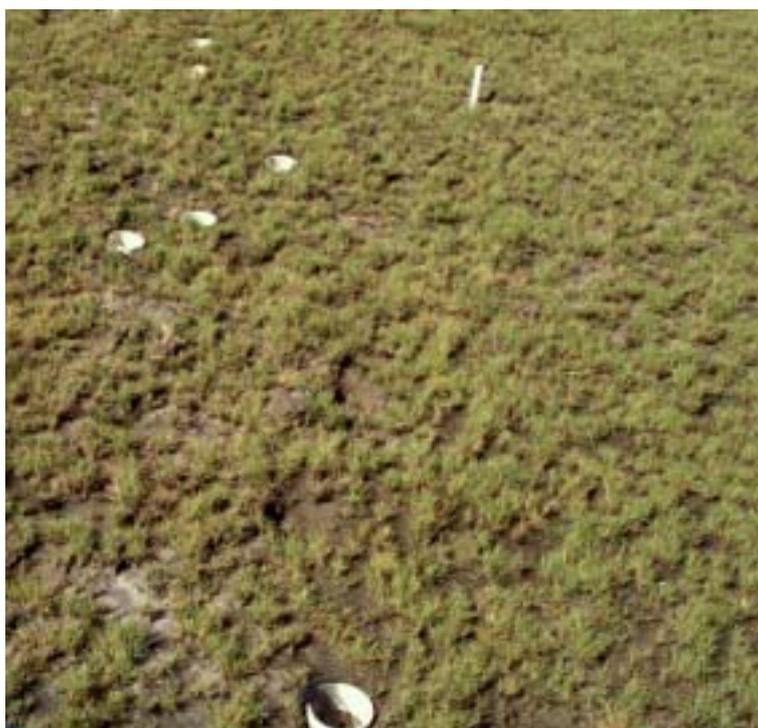


Figure 7. Pitfall traps set up in a treatment plot to sample ground-dwelling crabs and other mobile epibenthos.

2.3.3 Stable isotope analysis of sediment and major consumer

The pattern of carbon and nitrogen utilisation by grapsid crabs, a key group of consumers on the salt marsh, was assessed by stable isotope analysis. Different primary producers have characteristic stable isotope signatures for C and N, usually designated as ^{13}C and ^{15}N , defined as (for C)

$$\delta^{13}\text{C} = \frac{R_{\text{sample}} - R_{\text{std}}}{R_{\text{std}}} \times 1000$$

where R_{std} and R_{sample} stand for the ratio $^{13}\text{C}/^{12}\text{C}$ for the standard and sample, respectively. The standards used were calibrated regularly against the primary standards, namely, Pee Dee Belemnite limestone and atmospheric nitrogen, respectively, for C and N.

Samples of the grapsid crab *Helograpsus haswellianus* (Whitelegge 1889) were collected by hand from the experimental plots in 2002. The crabs were killed by freezing immediately after collection. Muscle tissues were extracted from the chelae of individual crabs, the samples were then dried at 60°C for >48 h, and ground for stable isotope analysis. The analyses were made using a continuous flow isotope ratio mass spectrometer, which has a precision of <2% for standards at most times. Source of nutrition of the crabs was ascertained by comparing the crab's signatures with those of the locally available primary producers, namely, the mangroves, *Sporobolus virginicus*, and benthic microalgae. The signatures of these producers are available from previous and concurrent studies carried out in the same area (e.g. M. Guest, unpubl. data).

2.3.4 Carbon and nitrogen contents of the sediment

Sediment carbon and nitrogen contents were analysed using the isotope ratio mass spectrometer, which was calibrated against standards regularly during the measurement process.

2.4 Data treatment and statistical analysis

Data on species abundance were used to calculate species diversity and evenness values for the assemblages. The Shannon species diversity index H' , defined as

$$H' = \sum_1^S p_i \log_2 p_i$$

where S is the total number of species in a sample, and p_i the numerical contribution of species i to the sample. Evenness J , which is a measurement of the degree of equitability of abundance among component species in a sample, is defined as

$$J = \frac{H'}{\log_2 S} \quad (\text{Pielou 1975})$$

The indices were calculated using Primer version 5 (Plymouth Laboratories 2001). Differences in the assemblages were tested by ANOSIM in Primer, using treatment (mowed, control) and size of the plots (20, 10, 5m) as the factors in a two-way crossed analysis (Clarke & Warwick 1994). Preliminary results from multi-dimensional scaling (MDS) analysis suggested that the factor of distance from the edge of the plot (the “Ring” factor) was relatively unimportant in separating the samples, and so attention was focussed on the effects of Treatment and Plot size in the comparison. The number of permutations performed was 999 in all cases. The null hypothesis was that there is no difference between the assemblages. A similar matrix among the samples was generated based on presence and absence data using the Bray-Curtis similarity measure, defined as (Bray & Curtis 1957) for separate series of core,

SAMS and pitfall samples for the 6 sampling rounds. Only presence/absence data were used because the counts of species abundance for the samples were not large, but often with a large proportion of zeros.

The similarity matrix calculated based on the species abundance data is used to generate a statistic, the Global R, which varies between 1 and -1. R is then compared to a distribution of R values generated by 999 random permutations of the data set. The null hypothesis is rejected when the calculated Global R is larger than 95% (i.e. >950 of the values in a 999-permutation test) of the values generated by the permutations.

Multidimensional scaling (MDS) was performed on the species abundance data also using Primer. MDS plots were generated using the similarity matrix using presence/absence data and Bray-Curtis similarity measure. Hierarchical cluster analysis was also performed in some cases to confirm affiliation of the samples after MDS.

Abundances of animals collected in the macrobenthos, SAM and pitfall samples were compared using the generalised linear model, with the factors of Treatment (fixed, 2 levels: Control/Treatment), Plot size (fixed, 3 levels: 5, 10, 20m) and Sampling Round (repeated, 6 levels). By specifying Sampling round as a 'repeated' factor, the analysis tests for significance differences between data from successive sampling rounds. The factors of Site and Ring (outer, middle and inner) were not included in the final analysis as preliminary analysis of the data suggested that they did not seem to exert a significant effect and so data for these factors were pooled in the analysis. The analyses were performed using SPSS version 12.01.

Data on the stable isotope signature of *Helograpsus haswellianus* and the sediment, and their carbon and nitrogen contents were analysed using a paired t-test.

Animals and sediment samples that were obtained from the same plot size/location combination were paired up for analysis, to minimise the effects of significant local influences on the conditions of the crabs.

3. RESULTS

3.1 General observations

Regeneration of *Sporobolus virginicus* was fast, with significant regrowth of the surface vegetation soon after the initial disturbance (Figure 8). Regrowth of the shoots attained ~5cm after just 2 months. After 5 months, some areas remain to be bare and without any regeneration but most shoots regrew to about 8cm but there was considerable difference among the 3 locations. Regrowth at location EN was slow, and was negligible in the 5m plots up to this time.



Figure 8. A 20m treatment plot on Cobby Cobby Island 5 months after the initial disturbance. Note that there are significant gaps in vegetation in the plot compared to the areas outside the boundary (indicated by the white arrows).

3.2 Aboveground biomass of *Sporobolus virginicus*

The mean initial aboveground biomass of *Sporobolus virginicus* was 356.26 ± 80.92 , 206.85 ± 109.68 and 345.21 ± 155.41 g dry wt m⁻² at, respectively, the CC, EN and ES locations (Figure 9). The values are not significantly different from each other (Kruskal Wallis one-way non-parametric ANOVA, $p=0.288$).

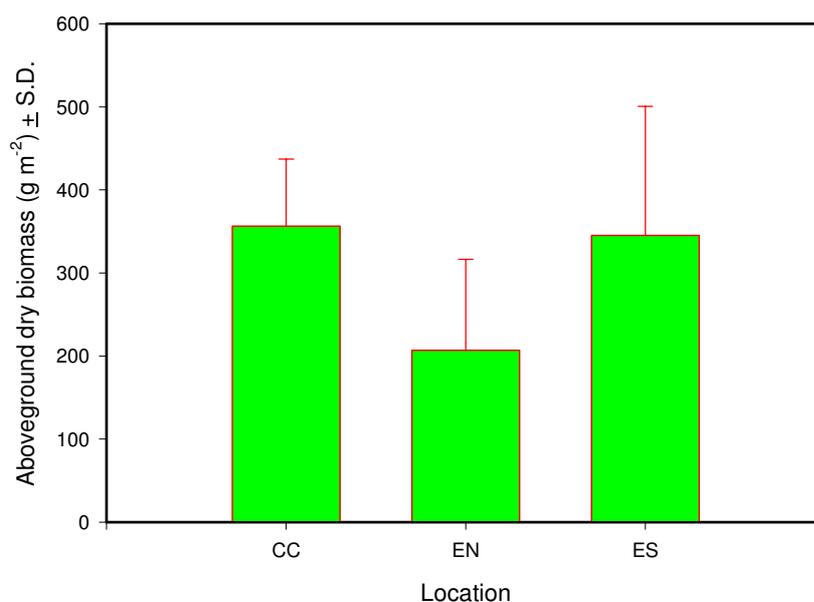


Figure 9. Dry aboveground biomass of *Sporobolus virginicus* meadows at the three study locations in November 2001.

3.3 Macroinvertebrate assemblage

The salt marshes supported rather impoverished animal assemblages, with the total number of species recorded (species richness S) in any single sample being <16 , with

the pitfall traps returning the highest average number of species per sample (4.6) (Table 1). A total of 100 morphospecies of animals have been recorded from the 3 types of samples, with 46, 11 and 85 species respectively from the core, pitfall and SAMS samples. Dominant species include the grapsid crabs *Helograpsus haswellianus*, *Parasesarma erythodactyla* and *Australoplex tridentata*, the littorinid gastropod *Littoraria philippiana*, the prosobranch *Assiminea buccinoides* and the pulmonate *Salinator solida* often are abundant; the gastropods typically found clustered around the base of culms of *Sporobolus virginicus* or in the burrows of the grapsid crabs. This behaviour is probably an adaptation to reduce desiccation stress on the salt marsh during long aerial exposure during the neap tide period.

Table 1. A summary of the species richness S , total number of individuals N , Shannon diversity H' and Pielou's evenness J' for the three types of samples collected during the experimental period. Values given are the maximum values and means.

	S	N	H'	J'
Cores	8, 2.6	68, 7.7	2.73, 0.96	1, 0.83
Pitfall Traps	8, 1.3	53, 4.6	2.36, 0.37	1, 0.83
SAMS	15, 4.3	2187, 34.7	2.90, 1.30	1, 0.73

3.3.1 Macrobenthos

Univariate comparisons of the assemblage parameters of species richness, abundance, Shannon diversity and Pielou's evenness indicate that sampling round had a

significant effect on these parameters, while mowing treatment alone generally had no significant effect (Table 2). Examination of the contrast on the 'Round' factor when a significant effect of this factor was obtained indicates that most of the significant differences occurred between Round 2/Round 3, i.e. <4 months post treatment in the treatment plots.

Significant interaction terms in the analysis mostly involved the Round*Treatment combination (Table 2). This suggests that the assemblage parameters varied in a temporal fashion significantly different between the treatment and the control plots. This result, combined with the results of the contrast within the Round factor, indicating that there was probably some short-term effect of the treatment after the mowing treatment.

Table 2. A summary of the significance levels of 3-factor ANOVAs performed on the core sample data, testing for the effects of sampling round, treatment and plot size on species richness (*S*), abundance (*N*), diversity (*H'*) and evenness values (*J'*).

Significant results at the 5% level are highlighted in bold.

	<i>S</i>	<i>N</i>	<i>H'</i>	<i>J'</i>
Sampling round (R)	<0.001	<0.001	0.124	<0.001
Treatment (T)	0.526	0.737	0.453	0.151
Plot size (S)	0.087	0.843	0.055	0.060
Significant interactions	R*T	None	R*T*S	R*T

Multivariate comparisons of the macrobenthos assemblages using ANOSIM resulted only in a significant Plot size effect in Round 2 (Global R = 0.191, p =0.001). Global R values for Treatment varied between -0.028 to 0.055 and were all non-significant at the 5% level.

This pattern is confirmed by the multidimensional scaling plots (Figure 10). Plot size was the best factor explaining the group pattern, while Treatment and Ring did not seem to be important in determining group membership.

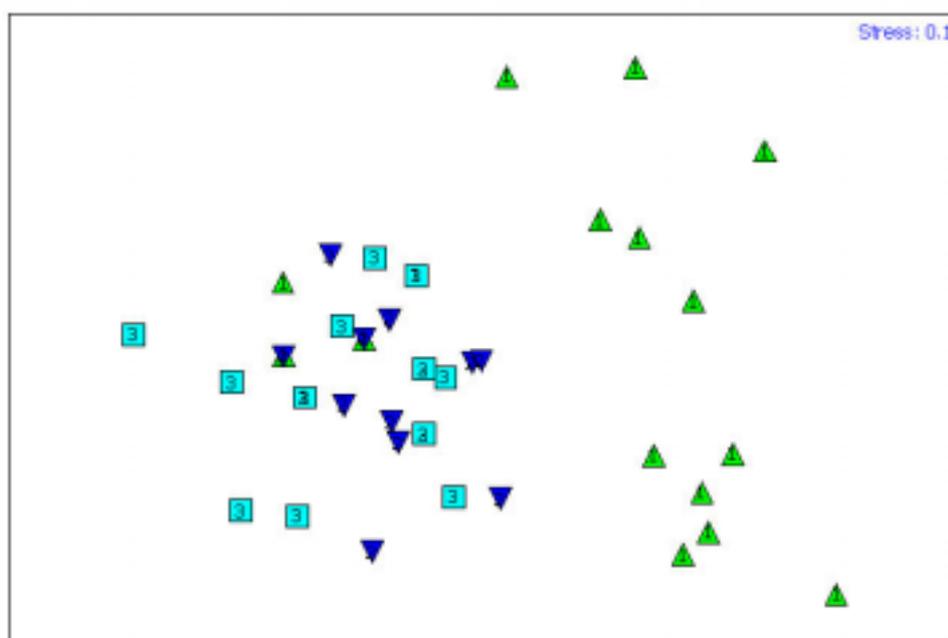


Figure10. A MDS ordination of the core samples for Round 2 based on presence/absence species abundance data and Bray-Curtis similarities. '1', '2' and '3' respectively represent the 5, 10 and 20 m plots.

3.3.2 Mobile epibenthos

Mobile macrobenthos of the salt marsh plots as recorded by the pitfall traps were dominated by ground-dwelling grapsid crabs (Figure 11) and gastropods, with occasional occurrence of other small crustaceans.



Figure 11. Two of the dominant epibenthos species on the salt marshes, the grapsid crab *Helograpsus haswellianus* and the pulmonate gastropod *Salinator solida*.

Unlike the core samples, which recorded the less mobile macrobenthic assemblage, the pitfall data do not suggest any effect other than that of Sampling round. Also, there were no significant interaction terms. Examination of the Sampling round data suggests that all the difference occurred between Round 5 and Round 6, indicating that this difference is more related to the sampling time than impact of the mowing treatment.

Multivariate comparison of the assemblages in a two-factor crossed ANOSIM resulted only in a significant difference due to Plot size in Round 2 (Global $R = 0.125$, $p = 0.021$). Pairwise comparison further indicates that the difference occurred between the 5 and 10m plots ($p = 0.027$). Global R values ranged from -0.007 to 0.125 for the Plot size factor, and between -0.037 to 0.094 for Treatment.

Table 3. A summary of the significance levels of 3-factor ANOVAs performed on the pitfall trap sample data, testing for the effects of sampling round, treatment and plot size on species richness (S), abundance (N), diversity (H') and evenness values (J'). Significant results at the 5% level are highlighted in bold. Since Round 4 did not record any animals, data for this round were excluded from the analysis.

	S	N	H'	J'
Sampling round (R)	<0.001	0.001	<0.001	0.016
Treatment (T)	0.590	0.883	0.443	0.163
Plot size (S)	0.900	0.866	0.977	0.641
Significant interactions	None	None	None	None

Distinct groups of samples are discernable in the MDS plot for Round 2 (Figure 12). Although Treatment seems to provide a good explanation of the some of the groupings, there is still considerable presence of Treatment samples in the clusters formed by the Control samples.

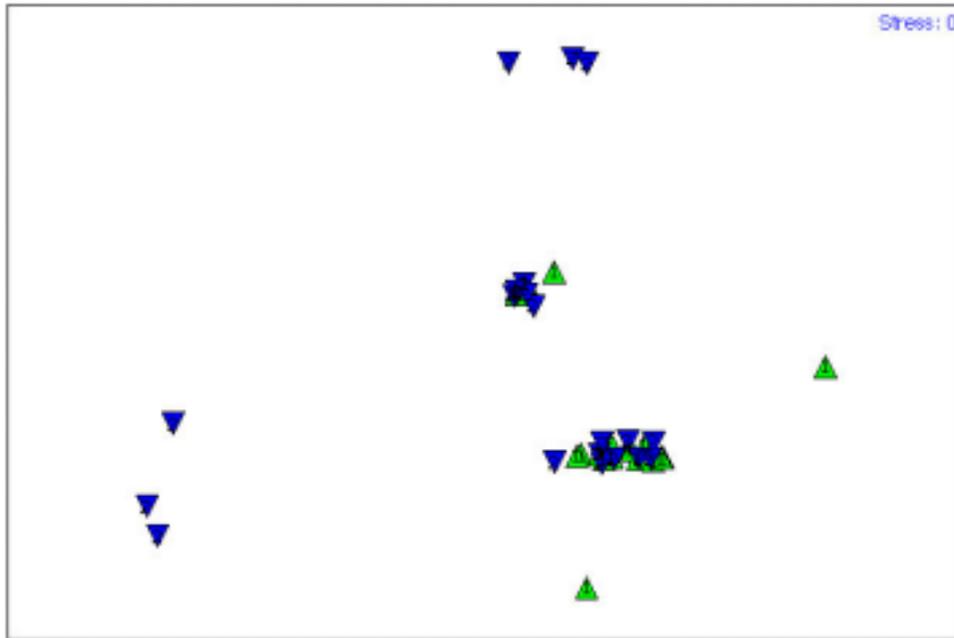
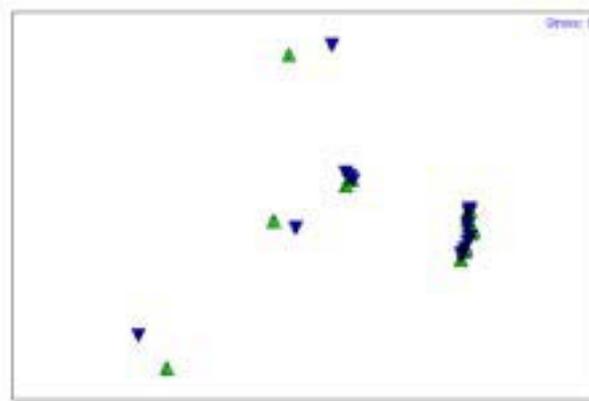
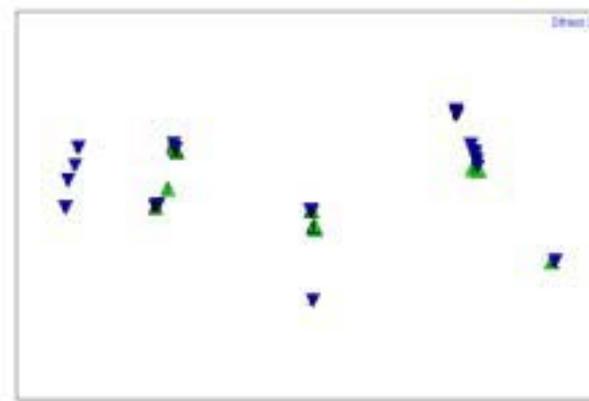


Figure 12. MDS ordination of presence/ absence pitfall trap data for Round 2. Good separation is achieved, but none of the three factors, namely, Treatment, Plot size or Ring provide a good explanation of the grouping. Treatment, presented here (▲ – Control, ▼– Treatment; shown here as labels for the samples) provides the best agreement with the groupings, but there is still substantial overlap in group membership.

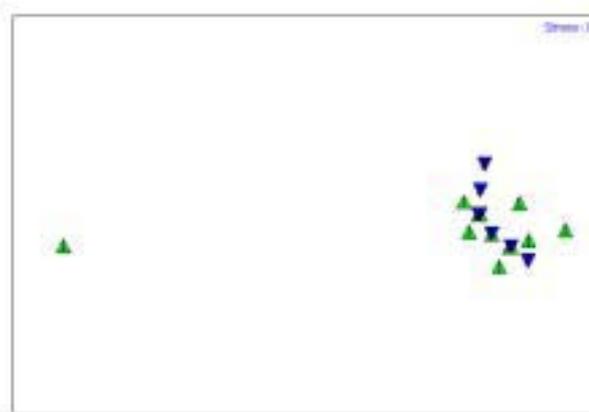
Examination of the MDS plots for the other sampling rounds suggests that some unknown factor(s) was influencing the pitfall trap catches, although the nature of these factors is unclear (Figure 13). The stress values of these ordinations are all <0.1, generating clearly discernable groups that are not directly related to any of the 3 factors tested.



Round 3



Round 5



Round 6

Figure 13. MDS ordinations of pitfall trap data for Rounds 3, 5 and 6. Good ordination was obtained in all cases, but Treatment (▲ – Control, ▼ – Treatment; shown here as labels for the samples) did not explain the groupings.

3.3.3 SAM samples

The assemblages collected by the SAMs were generally more variable both in species richness, abundance and composition. The mean number of species recorded per sample was 4.3, with 34.7 individuals. Evenness was generally high, averaged at 0.73, but diversity was low (1.30) because of the small number of species usually present.

Table 4. A summary of the significance levels of 3-factor ANOVAs performed on the SAM sample data, testing for the effects of sampling round, treatment and plot size on species richness (S), abundance (N), diversity (H') and evenness values (J').

Significant results at the 5% level are highlighted in bold. Since Round 5 did not record any animals, data for this round were excluded from the analysis.

	S	N	H'	J'
Sampling round (R)	<0.001	0.294	<0.001	<0.001
Treatment (T)	0.879	0.517	0.586	0.090
Plot size (S)	0.015	0.167	0.130	0.019
Significant interactions	None	None	None	None

The contrast results suggest that there was significant difference between Round 4 and Round 6 samples (Round 5 was absent). Pairwise comparisons of the 3 plot sizes where a significant Plot size effect occurred indicated that significant differences existed between 10 and 20m plots for S and J' .

None of the ANOSIM tests were significant for the factors of Treatment and Plot size for the SAM samples. There was no significant difference between the

assemblage structure of the samples according to these two factors. The equality of the assemblages is confirmed by the MDS plots, most of which have large stress values (~0.20, Figure 14).

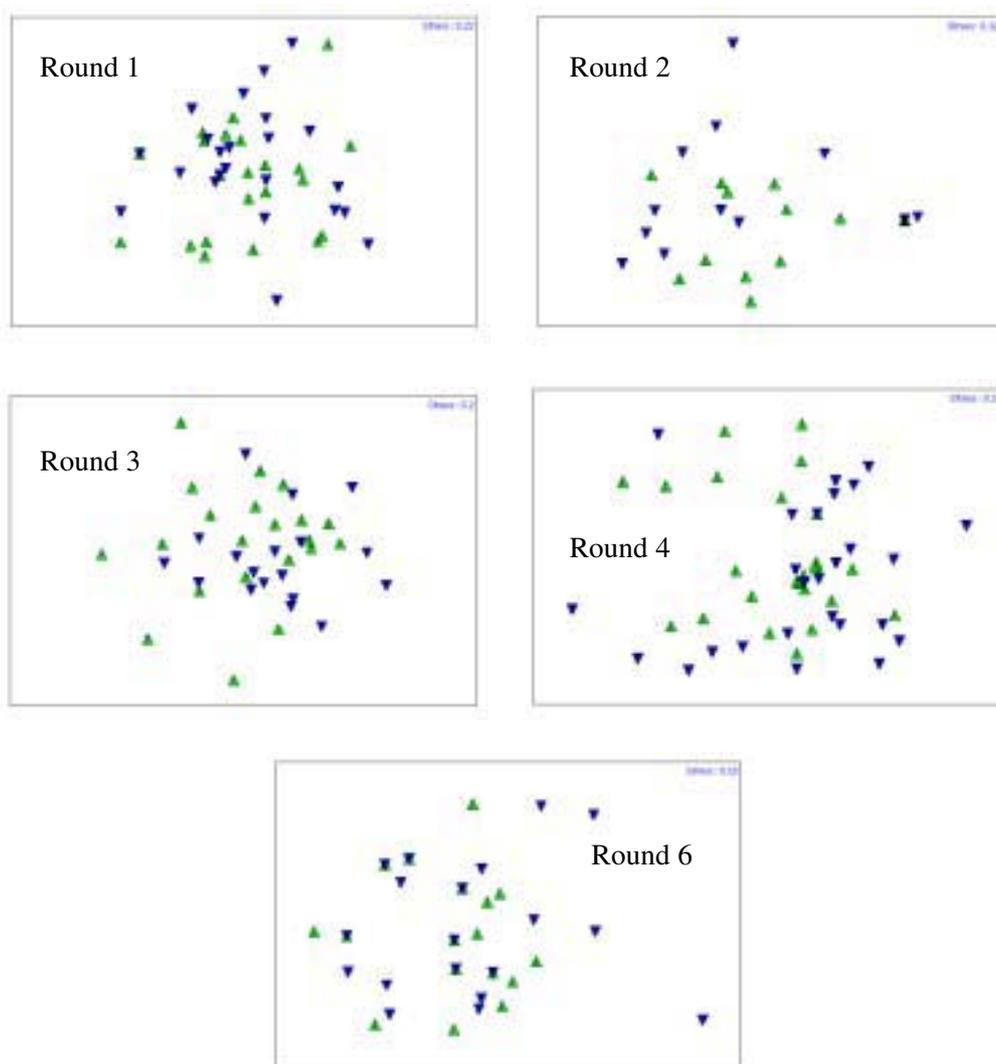


Figure 14. MDS ordination of the SAM samples based on presence/absence data. Treatment (▲ – Control, ▼ – treatment; shown here as labels for the samples) fails to explain the groupings, nor do Plot size or Ring.

3.4 Stable isotope analysis

Crabs collected from the Control plots generally had a lower % carbon and % nitrogen content than their counterparts from the same plot size/location combination, but probably because of the small sample size (n=9), the differences were not statistically significant (Table 5). The stable isotope signatures of the crabs were similar, suggesting that they were broadly dependent on the same food sources irrespective of whether they were in the Control or Treatment plots.

Table 5. Results of chemical analyses of the tissues of the grapsid crab *Helograpsus haswellianus* collected from the Treatment and Control plots.

	% Carbon	% Nitrogen	¹⁵ N (‰)	¹³ C (‰)
Control plots	33.3±2.9	11.32±1.1	5.3±2.4	-14.9±1.1
Treatment plots	31.6±1.8	10.6±0.7	4.2±1.2	-14.6±1.0
p for paired t-test	0.111	0.072	0.602	0.184

3.5 Carbon and nitrogen contents of the sediment

The mean carbon and nitrogen contents of the sediment in the Control plots were, respectively, 21 and 24% higher than those in the Treatment plots. However, because of the relatively large variability, paired t-tests did not record any significant differences (Table 6). Variability in the stable isotope signatures of carbon and nitrogen was even larger, but the mean values of the Control and Treatment plots were close.

Table 6. Carbon and nitrogen contents, and the stable isotope signatures of sediment samples from the experimental plots.

	% Carbon	% Nitrogen	¹⁵ N (‰)	¹³ C (‰)
Control plots	1.56±0.92	0.14±0.08	2.56±0.94	-16.9±0.97
Treatment plots	1.29±0.68	0.11±0.06	2.43±1.03	-16.8±0.99
p for paired t-test	0.246	0.195	0.703	0.613

4. DISCUSSION

4.1 Aboveground biomass of *Sporobolus virginicus*

Sporobolus virginicus is a cosmopolitan species in subtropical and warm temperate salt marshes. Numerous races of *S. virginicus* have been identified around Australia (Smith-White 1988). There are significant variations in growth form, in response to environmental and genetic differences (Donovan & Gallagher 1985, Smith-White 1988, Naidoo & Naidoo 2000). These variations are expected to result in differences in standing crop biomass and productivity. Day et al. (1989) reported end-of-season standing crop biomass of between 418 to 756 g dry wt m⁻² for salt marshes on the US Atlantic coast, with an average of 620 g dry wt m⁻². High standing crop biomass values have also been recorded by Dame & Kenny (1986) and Linthurst & Reimold (1978) for specific species of salt marsh plants along the US Atlantic coast. The average of 302.8 g dry wt m⁻² is small compared to most these figures. *Sporobolus virginicus*, being a small species, is expected to support lower aboveground biomass compared to *Spartina* spp., which dominate the Atlantic salt marshes of the US. Linthurst & Reimold (1978) reported aboveground biomass for *S. virginicus* at

between 119 to 578 g dry wt m⁻² in Georgia, USA. The level recorded in the present study is therefore in the centre of this range.

The fact that the aboveground biomass is small might imply differences in microhabitat conditions (e.g. humidity levels and temperature range) and food availability to animals associated with the habitat. The resilience of the salt marsh to disturbance such as removal of surface vegetation is probably affected by the ratio of aboveground to below-ground biomass of the species. These differences in physiognomy, microhabitat condition and general robustness between the Australian and Atlantic salt marshes that may influence their response to anthropogenic disturbances.

4.2 Effect of removal of vegetation on the macroinvertebrate assemblages

Studies on the resident animal assemblages of salt marshes are comparatively rare, let alone their relationship with anthropogenic disturbances such as the removal of surface vegetation. Recently, however, increasing attention is paid to the restoration of coastal wetlands, one important aspect of which is the development (or return) of the associated fauna of rehabilitated habitats. Usually long time periods (up to >10 years) are required for the faunal assemblages to attain equality, if ever, with natural undisturbed wetlands (Lee 2001). Many evaluations of the return of salt marsh associated fauna are, nevertheless, flawed in the methodology. Many have improper or single 'control' sites, and most are 'natural' experiments without proper experimental design to address the question of recovery. The manipulative experiment conducted in this study attempted to test the resilience (i.e. the ability of an ecosystem to recover from disturbance) and stability (i.e. the rate of recovery) of the *S. virginicus* salt marsh to a surface disturbance.

4.2.1 *Macrobenthos*

The macrobenthos assemblage recorded at the salt marshes is similar to their counterparts in other salt marsh systems. Lui et al. (2002) reported a total of 46 macrobenthos species (using a 500 m mesh), equally dominated by the polychaetes, molluscs, crustaceans and insects, from an impounded salt marsh in Hong Kong. Al-Khayat & Jones (1999) reported 23 species from the salt marshes of Qatar, dominated by decapod crustaceans and gastropod molluscs. It is not surprising that the Qatar assemblage is more species poor compared to southern Moreton Bay, as the former habitat is typically arid, with year round high temperature, high evaporation and low rainfall (55-76 mm y⁻¹). Forty-one taxa (250 m mesh) were recorded by Sacco et al. (1994) in a survey of 14 natural and artificial marshes in North Carolina, the Atlantic coast of USA. The smaller mesh size used in the present study (125 m) would have inflated the total number of species recorded.

The abundance of the local salt marsh macrobenthic species is, however, considerably lower than in similar systems elsewhere. Lui et al. (2002) recorded maximum densities of molluscs, polychaetes, and crustaceans at, respectively, 14440, 1973, and 16280 individuals m⁻² in a Hong Kong tidal marsh. Equally high infauna density (mean = 41759 individuals m⁻²) was reported by Sacco et al. (1994) for natural salt marshes in North Carolina. In a study of created salt marshes of different ages also in North Carolina, Craft (2000) reported mean densities of oligochaetes, a major component of the meiofauna in Atlantic salt marshes (Kneib 1984), reaching between 10000 – 30000 individuals m⁻² for marshes 20 y or older. The core samples in this study recorded maximum and mean density of macrobenthos at, respectively, 8568

and 980 individuals m⁻² for the entire assemblage, which are an order of magnitude lower than the values in North Carolina and Hong Kong.

Despite the relatively low abundance of the local salt marsh macrobenthos, the assemblage seemed to be able to recover from the applied disturbance in a relatively short time. Univariate analyses of species richness (S), abundance (N), diversity (H') and evenness (J') indicate that Treatment did not have an overall effect on these assemblage parameters, while significant temporal differences existed, as reflected by a significant ‘Round’ effect. Further examination of the difference suggests that the main difference existed between Rounds 2 and 3, which may point to a change in the assemblages in the initial period after disturbance. There is, however, no significance difference between the assemblages pre-disturbance (Round 1) and immediately after disturbance (Round 2), so this difference between Rounds 2 and 3 may be a result of other concomitant changes, such as changes in microhabitat conditions associated with the summer period, e.g. the hydroperiod and temperature. For three of the four parameters (except N) there are also significant interactions involving the Round and Treatment combination, suggesting that there was some difference in temporal pattern due to the treatment applied.

4.2.2 *Mobile epibenthos*

Decapod crustaceans and gastropods constituted the major taxa in the pitfall trap samples. Grapsid crabs are known to play an important functional role in tropical and sub-tropical coastal wetlands, particularly mangroves, in the Indo-west-Pacific (Lee 1998), but their significance to high intertidal salt marshes is relatively less known in the region. Ocypodid crabs, mainly *Uca* spp. and some predatory xanthids exert strong influences on ecological processes in the Atlantic salt marshes in terms of,

respectively, shaping the physical habitat structure through bioturbation (e.g. Bertness 1985) and predation of other species (Kneib 1997a). Compared to the local mangroves, the mobile epibenthos assemblage of the salt marsh plots was less species rich and less abundant. The number of species and individuals captured in the pitfall traps was generally approaching 4 and 20, respectively, in the study of mangroves by Lee et al. (2003), compared to only ~1 and <5 in the present study.

The mobile epibenthos assemblages in the experimental plots demonstrated significant temporal variation, especially towards the end of the experimental period (Table 3 and Section 3.3.2) but Treatment generally had no impact on assemblage diversity pattern. Unlike the case of the macrobenthos, there is no significant interaction between sampling time and treatment, further suggesting that Treatment did not have a strong impact on the structure of the mobile epibenthos. The composition of the assemblages was also not affected by the Treatment, as ANOSIM analyses did not register a difference according to this factor.

MDS ordination of the pitfall samples resulted in, however, strong grouping patterns throughout the sampling period (Figure 13). The groupings were nevertheless unrelated to any of the three factors examined, i.e. Treatment, Plot size and Ring (location in plot). These patterns suggest distinct 'sub-groups' of the mobile epibenthos existed in the plots, probably responding to the local microhabitat conditions such as vegetation cover (but not biomass) and organic matter content, factors that have been shown to influence the associated fauna in salt marshes (e.g. Fell et al. 1991, Craft 2000, Lui et al. 2002).

4.2.3 Juvenile nekton and plankton

As mentioned above, the SAM samples recorded the highest level of similarity amongst the various combinations of factors investigated (Figure 14, and results of ANOSIM analysis). Kneib (1997b) argued that the spatial variation of juvenile life history stages of resident nekton in salt marshes is different from that of more planktonic ocean-spawned species, the former group often being more responsive to local microhabitat factors such as tidal position. In the present study, however, the bulk of the taxa collected in the SAMs were organisms that do not show a strong demersal larval or juvenile phase. Consequently, it is not surprising that the samples do not show strong trends in time or space but are generally homogeneous across the experimental plots. Again, only the factor of 'Round' was significant in influencing the *S*, *H* and *J*' values, but only between Rounds 4 and 6. This late occurrence of a significant effect is probably unrelated to the treatment, which occurred >6 months earlier.

4.2.4 Response of salt marsh macroinvertebrate assemblages to disturbance

In a parallel study conducted on 4 mangrove forests in southern Moreton Bay, Lee et al. (2003) reported that amongst the three faunal sample groups monitored (macrobenthos, mobile epibenthos and SAMs), the macrobenthos were probably most indicative of local habitat conditions because of their more direct dependence on the physical habitat. This pattern seems to hold true in this study, as MDS ordination was least successful in separating the samples at any sampling period (Figure 14) for the SAM samples. This is probably due to the fact that planktonic organisms and juvenile nekton that are collected by the SAMs are most influenced by local hydrodynamics such as tidal flow, rather than a permanent association with the substrate. Disturbance

in the form of removal of surface vegetation may influence hydrodynamics through altered retention pattern of plankton (Mnaya & Wolanski 2002), but the impact is expected to be weaker than that on more substrate dependent organisms such as the macrobenthos or mobile epibenthos.

Kaly et al. (1997) found negative significant effects of tree removal and the associated soil disturbance on the nutrient (N, P) concentration and crab burrow density in a north Queensland mangrove. Crab burrow density decreased by >50% in severely damaged forests, and this, combined with the changes in nutrient concentration, is expected to exert strong consequences on forest function. In contrast, removal of salt marsh surface vegetation in the present study did not register any significant impact on the faunal assemblage. If any significant impact had occurred, the effects would have disappeared very soon after the initial disturbance, as the temporal samples failed to record a significant difference even early in the experimental period.

The severity of the disturbance that occurred in the two studies is, however, quite different. Being lower in the tidal gradient, mangrove sediment generally contains a much higher water content and is thus more susceptible to compaction. Surface vegetation removal is a more dramatic disturbance in a mangrove forest than a short salt marsh dominated by *Sporobolus virginicus*. It is of particular interest, therefore, to compare the responses of the Australian salt marshes to this disturbance with their Atlantic counterparts, which have a more robust aboveground structure.

4.3 Carbon and nitrogen contents and stable isotope signature of the sediment

No significant differences were detected in the C, N contents and the carbon and nitrogen stable isotope signatures of the sediment between the treatment and control

plots (Table 6). Some effect probably occurred as a result of the removal of surface vegetation, as there was a consistent (though statistically non-significant) trend of the Control plots having a higher C and N content compared to the Treatment plots. Removal of surface vegetation would result in the short-term absence of local organic production, and thus input of detrital matter to the sediment. Further, aboveground structures such as culms of *Sporobolus virginicus* could also help trap autochthonous detritus particles more effectively than bare substrates. Notwithstanding, the effect is probably too weak to be registered by the present comparison.

The isotopic signatures of the sediment suggest that the two sets of plots provide the same organic C and organic N sources to consumers. The ^{13}C and ^{15}N values of the two sets of plots were almost identical, showing values typical of a mixture dominated by *S. virginicus* detritus, with some contribution from a more depleted carbon source. *S. virginicus* has a ^{13}C of between -14 to -15‰ in southern Moreton Bay (Guest et al. 2004). The other significant end member is likely to be either mangroves (-27 to -29‰) or benthic microalgae (-14 to -20‰), with the latter a more probable local source.

4.4 Stable isotope signature of *Helograpsus haswellianus*

As the dominant macroinvertebrate present on salt couch meadows, *Helograpsus haswellianus* provides a good indication of any changes in the trophic ecology of the plots subsequent to the treatment. Crabs obtained in paired plots demonstrated no significant differences in all 4 parameters measured, although there are signs that crabs within the Control plots generally had better body conditions, as reflected by marginally higher tissue %C and %N. This trend echoes that in sediment composition (see above).

The difference in stable isotopic signature for carbon (^{13}C) and nitrogen (^{15}N) were negligible between crabs from the two types of plots. Salt marsh crabs move over only small distances to forage (Lee, unpubl. data), their isotopic signature is therefore indicative of the local trophodynamic pattern within the plots. Guest et al. (2004) measured the carbon and nitrogen isotopic signature of *S. virginicus* in southern Moreton Bay at locations in the vicinity of the present study plots, and recorded signatures almost identical to those of *Helograpsus haswellianus* in this study. Despite some local variations due to the position of samples in patches (edge vs interior) or along the tidal gradient, ^{13}C of *S. virginicus* varied from -14.2 to -15.0‰ , and the mean ^{15}N was $5.5\text{‰} \pm 0.7$, with no significant spatial differences. *H. haswellianus* is probably directly dependent on either *S. virginicus* or the sediment organic C for food, as both sources have ^{13}C values that can explain the crab's signature, within the limits of expected trophic fractionation (McCutchan et al. 2003). The ^{15}N value also agrees with the range of values expected of a *S. virginicus* dominant diet, with a trophic shift of between $+2$ to 2.8‰ .

5. CONCLUSIONS

Experimental removal of surface vegetation in salt marshes dominated by *Sporobolus virginicus* in southern Moreton Bay did not result in any significant impact on the associated faunal assemblages over an 18-month period. The macrobenthos associated with the experimental salt marshes were comparable to other systems in terms of the number of species, but are impoverished in terms of abundance. Despite some weak indication of shifts in organic matter availability, surface vegetation removal also did not result in changes in the content and the sources of carbon and nitrogen of the sediment. Diet of the dominant mobile epibenthos, the grapsid crab *Helograpsus*

haswellianus, mainly supported by *S. virginicus* detritus, was also unaffected by the manipulation. Fast regeneration of *S. virginicus* probably contributed to the lack of long-term impact of the disturbance. The *Sporobolus* marshes were therefore resilient to the applied disturbance. However, because of significant differences in the physiognomy and thus, resilience and robustness between *S. virginicus* dominated marshes and the much better known Atlantic systems, further investigations into the response of Australian salt marshes to anthropogenic disturbances are warranted.

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