

# Effects of grazing by a marine mega-herbivore on benthic assemblages in a subtropical seagrass bed

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**ABSTRACT:** The effects of grazing by the dugong *Dugong dugon* on benthic invertebrate assemblages in seagrass beds were examined in subtropical Moreton Bay, southeast Queensland, Australia. During feeding, dugongs leave distinct trails through seagrass beds where vegetation has been removed and sediments disturbed. The abundance of benthic fauna was examined along 3 recently created feeding trails and compared to 3 nearby patches of ungrazed seagrass within the same bed. A controlled, manipulative field experiment was then conducted, simulating the effects of dugong grazing, but distinguishing between the effect of removal of vegetation and the disturbance of the sediment during feeding. Dugong grazing was associated with declines in the abundance of benthic animals by up to 85% along trails, with the most noticeable impacts on amphipods and polychaete worms. Simulated dugong grazing caused a significant decline in the biomass of seagrass, through the removal of the vegetation but also from the physical disturbance during feeding. The combined and separate effects on the vegetation and from disturbance were associated with: (1) significant effects of grazing but not of physical disturbance for amphipods, capitellid and opheliid polychaetes; (2) significant effects of physical disturbance with no additional effect of grazing for terebellid polychaetes; (3) significant effects of physical disturbance with an additional effect of grazing for tanaids, bivalves and sabellid polychaetes; (4) significant short-term effects after 1 wk, no longer apparent after 4 wk, for ostracods, nereidid and syllid polychaetes and nemerteans; and (5) no effect of grazing or physical disturbance for isopods and spionid polychaetes.

**KEY WORDS:** Dugong · Grazing · Subtropical seagrass · Benthic infauna

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## INTRODUCTION

Seagrass meadows are highly productive and dynamic coastal ecosystems that play a role in many different processes within estuarine ecosystems (e.g. Lanyon et al. 1989). They provide food, shelter and breeding and nursery grounds for numerous animals, including many of importance to commercial and recreational fisheries (Thayer et al. 1984). Seagrass communities may also act to trap sediments and organic nutrients (Ginsburg & Lowenstam 1958), providing an increased supply of detritus that is the staple food for animals within the seagrass beds. Direct grazing of seagrasses is often considered to be a relatively insignificant component of the utilisation of organic matter in seagrass beds, with few herbivores feeding on the seagrass material itself (Thayer et al. 1984). In

tropical and sub-tropical regions, however, large marine herbivores, including dugongs, green turtles and sea urchins, consume considerable amounts of seagrass material and may have a significant impact on seagrass communities (Best 1981, Kirkman & Young 1981, de Iongh et al. 1995).

Grazing by macro- and mega-herbivores alters rates of plant growth and species diversity, primary production, nutrient cycling, energy flow and age distribution in terrestrial plant communities (e.g. McNaughton 1979, Brown & Ewel 1987, Cyr & Pace 1993). These and other studies on terrestrial plant-herbivore interactions have demonstrated not only that grazing has a significant and lasting effect on plant communities, but also that there is the potential for cascading effects through the ecosystem, resulting in changes to associated animal communities (e.g. Baines et al. 1994, Bromham et

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al. 1999). The role of large herbivores in aquatic systems has not been studied as extensively as in terrestrial systems, yet the data that are available suggest that aquatic mega-herbivores may exert as much, if not more, influence on plant communities as their terrestrial counterparts (Cyr & Pace 1993, Cebrian & Duarte 1994). Grazers such as fish, sea urchins, turtles and dugongs have the capacity to modify the species composition, nutrient and fibre content, productivity, biomass, growth rate and regeneration of seagrasses (Lanyon et al. 1989, Preen 1995, Rose et al. 1999, Macia 2000, Kuiper-Linley et al. 2007).

The dugong *Dugong dugon* (Muller 1776) is the only strictly marine herbivorous mammal (Marsh et al. 1995), feeding almost exclusively on seagrasses (Lanyon et al. 1989) and consuming up to 10 to 15% of its body weight in seagrass daily (Best 1981). Dugongs are highly selective foragers, primarily consuming seagrasses of the genera *Halophila* and *Halodule*, which have greater digestibility and nutritional value compared to other species of seagrass (Aragones et al. 2006, Lanyon & Sanson 2006). Dugongs also eat some algae, especially when seagrass is sparse (Heinsohn & Spain 1974, Preen & Marsh 1995), although this may just be a product of incidental ingestion (Lanyon et al. 1989).

Dugongs are widely distributed in the Indo-Pacific region, between longitudes 30° and 170° E and latitudes 27° N and 27° S, inhabiting tropical and subtropical warm, shallow coastal waters (Marsh & Lefebvre 1994). Australia is the last stronghold of global dugong populations, with dugongs widespread throughout the northern waters of Australia and down the east and west coasts to approximately 27° S (Marsh et al. 1995). In the northern populations, dugongs are often solitary (Marsh & Saalfeld 1989) or in small herds (Preen 1995) but in Moreton Bay, the southern limit of the dugong's range, they often move in large herds of 100 to 300 animals (Lanyon 2003). Moreton Bay has a population of between 800 and 1000 dugongs, the majority of which are found in the eastern parts of the bay over shallow sandbanks inshore from Moreton and North Stradbroke Islands (Lanyon 2003). The dugongs in Moreton Bay feed predominantly on seagrass beds dominated by *Halophila ovalis* and *Halodule uninervis*, with herds sometimes grazing in a single location for up to 35 d (Preen 1995). This intensity of grazing results in changes to the composition of species of seagrass present on the banks and the nutrient availability, fibre content, age distribution and biomass of the seagrasses (Preen 1995).

Grazing by dugongs may also cause considerable short-term disturbance to the seagrass community. When feeding on their preferred seagrasses, dugongs dig up the entire plant, removing between 63 and 86%

of the available biomass and leaving distinct feeding trails (19 to 25 cm wide, 3 to 5 cm deep and 1 to 5 m long) through the seagrass bed (Lanyon & Sanson 2006). Their feeding also potentially causes substantial disturbance to the sediment as the plant material is removed. While it is known that intensive grazing can cause changes to the plants, it is not known whether there are any direct or indirect effects on the animal communities that are associated with the seagrasses.

Removal of seagrass—or changes to the structural complexity provided by the vegetation—due to grazing has implications for other organisms that use this spatially heterogeneous habitat as a refuge from predation (e.g. Coen et al. 1981, Summerson & Peterson 1984). The physical disturbance may lead to changes in the characteristics (e.g. granulometry, compaction) of the sediments, also influencing organisms in these habitats because of the close association between soft-sediment infauna and sedimentary parameters (e.g. Sanders 1958). There may also be a reduction in the stability of the sediments through a loss of features such as animal tubes (Woodin 1979) and the seagrass itself (e.g. Ginsburg & Lowenstam 1958). Disturbance of the sediments also has the capacity to cause direct mortality of infauna as a result of burial (e.g. Maurer et al. 1981). Any impacts associated with burial are likely to vary depending on the mobility of the animals (tube dwellers vs. mobile burrowers) and their feeding type (Brenchley 1981). The main objective of this study was to investigate the effects of dugong grazing on the abundance and composition of animal communities in seagrass beds in Moreton Bay. The study was also designed to determine whether any effects from grazing were due primarily to the removal of plants from the system (direct effects of grazing) or are a result of the disturbance to the sediments that occurs during feeding (indirect effects of disturbance). This was done using 2 complementary approaches structured to determine whether there were effects caused by individual dugongs on the benthic communities. First, the abundance and composition of benthic communities were compared between recently grazed trails and ungrazed seagrass beds. Second, a manipulative experiment was conducted in the field, simulating the effects of grazing by dugongs but partitioning any effects due to removal of the vegetation and those due to disturbance of the sediments.

## MATERIALS AND METHODS

**Study sites.** This work was done in seagrass beds located on the eastern side of Moreton Bay, southeast Queensland, Australia (27° S; 153° E; Fig. 1). This region of Moreton Bay is characterised by expanses of

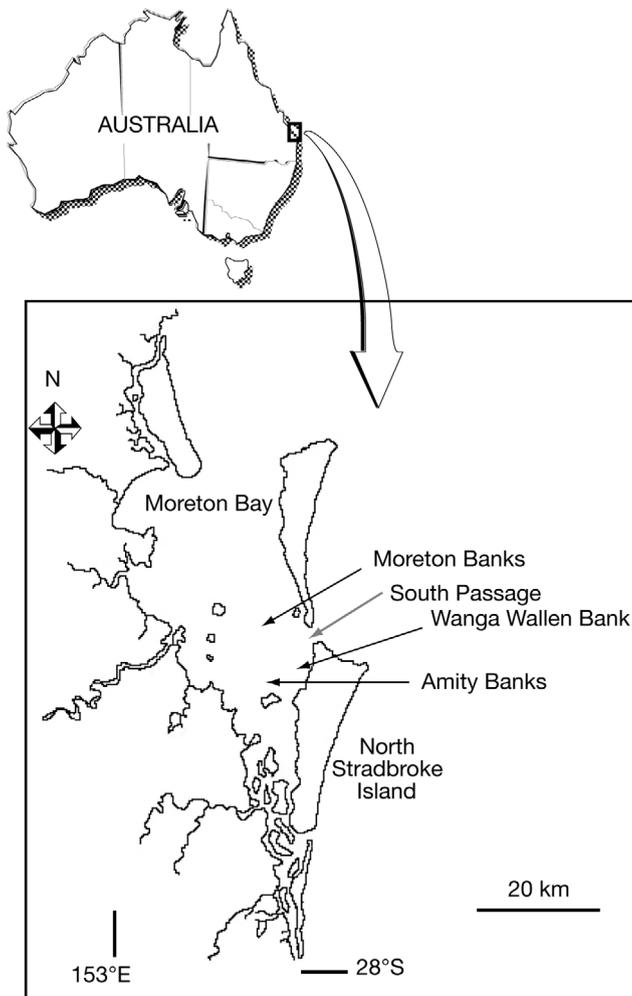


Fig. 1. Moreton Bay region of southeast Queensland, Australia showing the position of the sites in eastern Moreton Bay

shallow sand banks—Moreton, Amity and Wanga Wallen Banks—that support extensive seagrass meadows. Tidal intrusion of oceanic water through the South Passage (Fig. 1) maintains high water quality and clarity throughout this region, providing ideal conditions for the growth of seagrasses (Gabric et al. 1998). A variety of seagrass species are found throughout the region, including *Zostera capricorni*, *Halophila ovalis*, *H. spinulosa*, *Syringodium isoetifolium* and *Halodule uninervis* as the most common species, with *Halophila decipiens* and *Cymodocea serrulata* being considerably less abundant (Preen 1995). The seagrass meadows on these sand banks are the principal feeding grounds for dugongs and green turtles in Moreton Bay (Lanyon 2003).

**Small-scale effects of dugong grazing.** To determine whether the presence of feeding trails affects the composition of the epifaunal and infaunal communities in the seagrass, benthic cores were collected from a

series of recently created trails and from surrounding ungrazed seagrass. An aerial survey was done on 18 April 2000 to record positions of dugong herds in the eastern region of Moreton Bay. Five herds of 40 or more dugongs were sighted during the survey over Moreton and Amity Banks. The locations of the herds sighted from the air were then inspected by boat, and the intertidal area of Amity Banks with the most easily distinguishable fresh feeding trails was selected as the study site. The site had a relatively sparse seagrass cover and was dominated by *Halophila ovalis* and *H. spinulosa*. Three feeding trails were randomly selected from within the seagrass bed on Amity Banks. From each trail, 3 replicate sediment samples, each at least 30 cm apart along the trail, were collected using a hand-held corer (15 × 15 cm diameter × depth, volume ~2650 ml). Sediment samples were also taken from within the same seagrass bed but away from any trails. Three replicate cores were collected from each of 3 randomly selected patches of seagrass. Each of the seagrass patches was at least 25 m from the nearest trail and had no visible signs of having been recently grazed.

All sediment samples were fixed using formalin (5%) and stained with Rose Bengal, which targets biological material, allowing animals to be easily identified in the sample. The samples contained sediment, seagrass and the component organisms. The samples were sieved across stacked 1 mm and 500 μm sieves and then preserved in 70% methylated spirits until they could be sorted. Samples were divided into these 2 size categories to determine whether any effects of dugong grazing varied as a function of the different size groupings of infauna in the seagrass beds. Large numbers of nematodes and copepods were retained on the 500 μm sieve, but these were excluded from the data as these groups are more typical of the meiofauna (animals <500 μm in size) and may not be sampled effectively using these methods. The seagrass in each sample was removed for determination of biomass, and the epifauna and infauna were sorted to the lowest possible taxonomic unit. The seagrass removed from the samples was dried and weighed to determine the combined above- and below-ground seagrass biomass.

**Experimental simulation of dugong grazing.** A controlled, manipulative field experiment was carried out to determine whether differences in the numbers and types of animals in grazed (trails) and ungrazed (non-trails) areas could be attributed to the effects of dugong feeding or were more likely due to natural environmental variation among the grazed and ungrazed sites (i.e. confounding). The effects of dugong grazing were simulated in a seagrass bed on Amity Banks known to be grazed regularly by dugongs. To avoid the possibility that the dugongs would interfere

with the experiment or influence the results, the experiment was done in early August (2000), after the large herds had dispersed widely throughout the eastern bay (Lanyon 2003). Sampling of seagrass-associated fauna in beds elsewhere in Moreton Bay indicate no marked fluctuations in the abundance of benthic animals at different times of the year (Skilleter et al. 2006), so it is unlikely that the timing of this experiment would bias the generality of the results. The experiment was done at 2 separate sites approximately 1 km apart.

Three different treatments were used in the experiment: grazed plots, grazing control plots and ungrazed control plots. The grazing treatment involved removing 80% of the seagrass in the plot in a manner simulating dugong grazing. A garden rake was modified to correspond to the width of an adult dugong's muzzle (20 cm wide; 5 cm long tines). The rake was pulled 6 times across the length and 6 times across the width of the plot in a grid-like fashion. Seagrass, roots and rhizomes were removed to a depth of 5 cm below the surface of the sediment (similar to dugong grazing). A similar approach was used in the grazing control plots; however, the back of the rake was rubbed over the surface of the seagrass and sediment without removing any seagrass. This treatment was used to distinguish between the effects caused by the removal of the seagrass material during dugong feeding versus any effect related to the physical disturbance of the sediment associated with the feeding. The ungrazed control plots were left undisturbed. At each site, 24 plots, each 2 × 2 m, were marked with wooden stakes and coloured flagging tape. Eight replicate plots for each of the 3 treatments were randomly assigned among the 24 marked plots at each site. The intention was to sample 4 replicate plots (per treatment) after 1 wk and the other 4 remaining plots after 4 wk to allow examination of any temporal patterns in the effect of the simulated grazing on the benthic assemblages. At the appropriate times, 5 replicate sediment samples (15 × 15 cm diameter × depth, volume ~2650 ml) were randomly collected from within each of the 4 replicate plots per treatment. These samples were processed and sorted in the same manner as previously described. The seagrass in each sample was separated from the sediment during sorting, dried at 75°C to a constant weight and then weighed to determine total (above- and below-ground) biomass.

**Statistical analyses. Small-scale effects of dugong grazing:** Nested 2-factor analyses of variance (ANOVAs) were done to determine whether there were any significant differences between the abundance of animals in trails and non-trails. The factors in the ANOVAs were treatment ( $a = 2$ , fixed) and patches within treatment ( $b = 3$ , nested and random). The data

were log transformed ( $\log_e[x+1]$ ) to satisfy the assumption of homoscedastic error variances (Underwood 1981). Separate ANOVAs were done on the component of the fauna retained on the 1 mm sieve and the total number of animals retained on the 500 µm sieve.

The total number of individuals and any taxa that comprised >10% of the total number of individuals were analysed using univariate ANOVA. For the larger fraction (>1 mm size), analyses were done for numbers of gammarid amphipods, ostracods, bivalves and polychaetes. For the animals retained on the 500 µm sieve (including those retained on the 1 mm sieve), analyses were done for numbers of gammarid amphipods, ostracods, bivalves, polychaetes, cumaceans, tanaids and gastropods.

Differences in the community composition of the fauna between trails and non-trails were examined with non-metric multidimensional scaling (nMDS) on untransformed data, using the Bray-Curtis similarity measure (Clarke 1993). The statistical significance of any differences in the composition of the fauna between trails and non-trails was tested using permutational multivariate analysis of variance (PERMANOVA) using the permutation of residuals under a reduced model (Anderson 2004). Separate analyses were done on the data from the animals >1 mm (retained in a 1 mm sieve) and those >500 µm (retained on a 500 µm sieve). Correlation coefficients were calculated between the biomass of seagrass and the total abundance of animals and the abundance of individual taxa in cores collected from areas with trails and those without (non-trails).

**Experimental simulation of dugong grazing:** Although the experiment was established at 2 sites, not all samples could be processed from 1 of these sites, so 2 separate sets of analyses were done. All samples were available from the first site (Site A), allowing a balanced design to examine the effects of seagrass removal (simulated grazing) on the macrofaunal community 1 and 4 wk post-disturbance. At the second site (Site B), data were analysed to examine whether the composition of the macrofaunal community 4 wk post-disturbance were similar to those observed at Site A and hence examined the generality of any impacts from seagrass removal and/or the associated disturbance. Analyses were done on the entire macrobenthic community (>500 µm size).

## RESULTS

### Small-scale effects of dugong grazing

There was a clear pattern in the abundance of fauna in the areas that had been recently grazed compared to

nearby areas of seagrass untouched by the dugong herds. For larger (>1 mm) specimens, generally more animals were present in the ungrazed (non-trail) areas than the grazed trails, with the exception of the number of bivalves (Table 1). The abundance of animals in the ungrazed areas was 45 to 66 % greater than in the grazed areas.

The pattern was similar for the fraction of the fauna >500 µm in size (Table 1). There was no significant difference in the abundance of bivalves or cumaceans between the grazed and ungrazed areas, but for other taxa (i.e. gammarid amphipods, ostracods, polychaetes, gastropods and tanaids) there were significantly more animals in the ungrazed than grazed areas (Table 1). For cumaceans, the magnitude of the difference between the treatments was 64 % and for bivalves 10 %, but these were not significant. The abundance of animals in the ungrazed areas was up to 86 % greater than in the grazed areas (e.g. tanaids, Table 1).

Despite the large differences between treatments in the abundance of larger (>1 mm) animals for some taxa, there was no significant difference in the composition of the community between the grazed and ungrazed areas nor among the multiple plots within each treatment, despite the apparent separation of the treatments in the ordination (Table 2; Fig. 2A). However, there was a clear difference between the grazed and

Table 2. Non-parametric multivariate analyses of variance (PERMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in grazed (Trails) and ungrazed (Non-trail) areas of seagrass at Amity Banks. Data were unstandardised and fourth-root transformed; n = 3 cores in each of 3 plots per treatment (Trails versus Non-trails). PERMANOVA was done using permutations of residuals (see Anderson 2004 for full details)

Source	df	MS	F	p	Possible no. permutations
<b>Animals &gt;1 mm Full model</b>					
Treatment	1	793.73	1.50	0.268	2.4 × 10 <sup>4</sup>
Plots (Treatment)	4	530.65	1.63	0.097	1.9 × 10 <sup>8</sup>
Residual	12	325.32			
Total	17				
<b>Animals &gt;1 mm Plots pooled</b>					
Treatment	1	3173.57	4.30	0.0002	2.4 × 10 <sup>4</sup>
Residual	16	738.59			
Total	17				
<b>Animals &gt;500 µm Full model</b>					
Treatment	1	794.29	3.20	0.041	2.4 × 10 <sup>4</sup>
Plots (Treatment)	4	248.20	1.82	0.060	1.9 × 10 <sup>8</sup>
Residual	12	136.61			
Total	17				

Table 1. Mean (± SE) number of individuals in different taxa, sampled from tracks recently grazed by dugongs (Trails) and nearby ungrazed patches of seagrass (Non-trail) and sorted across a 1 mm or 500 µm sieve. N = 9 cores for each treatment (3 replicate cores from each of 3 trails or ungrazed patches). Results of ANOVAs comparing differences between treatments are shown as p-values (see text for further details)

	Trails Mean (± SE)	Non-trail Mean (± SE)	ANOVA
<b>1 mm sieve</b>			
All individuals	115.7 (± 8.6)	211.1 (± 19.2)	p < 0.001
Gammarid amphipods	30.8 (± 5.5)	64.1 (± 11.0)	p < 0.02
Ostracods	6.8 (± 1.5)	19.8 (± 3.3)	p < 0.02
Bivalves	14.1 (± 2.3)	12.8 (± 2.3)	p > 0.65
Polychaetes	32.8 (± 3.8)	60.1 (± 9.3)	p < 0.02
<b>500 µm sieve</b>			
All individuals	239.0 (± 23.2)	513.9 (± 50.1)	p < 0.02
Gammarid amphipods	48.8 (± 5.8)	129.2 (± 14.8)	p < 0.005
Ostracods	28.8 (± 4.5)	78.6 (± 9.3)	p < 0.05
Bivalves	38.3 (± 5.7)	50.8 (± 11.8)	p > 0.52
Polychaetes	56.4 (± 5.8)	106.3 (± 15.7)	p < 0.03
Cumaceans	3.6 (± 1.1)	9.9 (± 2.7)	p > 0.17
Tanaids	2.0 (± 0.8)	13.8 (± 3.7)	p < 0.03
Gastropods	12.0 (± 2.4)	26.3 (± 5.9)	p < 0.05

ungrazed areas in the composition of the entire macrofaunal community (>500 µm; Table 2; Fig. 2B).

The abundance of animals in the area was positively correlated with the biomass of seagrass present, although the strength of the correlation varied considerably among taxa. The total number of animals showed the strongest correlation with seagrass biomass (r = 0.78, p < 0.0001), but other groups including ostracods (r = 0.75, p < 0.0002), tanaids (r = 0.74, p < 0.0003), bivalves (r = 0.71, p < 0.0007) and polychaetes (r = 0.70, p < 0.0009) were also more abundant in patches with a greater biomass of seagrass. The abundances of other groups such as gammarid amphipods (r = 0.42, p > 0.08) were not correlated with the biomass of seagrass.

### Experimental simulation of dugong grazing

#### Effects on seagrass biomass

At Site A, the experimental removal of seagrass decreased the biomass of vegetation by 86% in the grazed plots compared to the unmanipulated (ungrazed) plots (Table 3). The biomass of seagrass in the grazing control plots was reduced by 32% compared to the ungrazed plots, even though no seagrass was deliberately removed during the application of the experimental treatment. The reduction in seagrass in the grazing control

plots presumably arose from destabilisation of the sediments with subsequent loss of vegetation through erosion of the sediments under tidal and wave-driven water movement. All 3 treatments were significantly different from each other with respect to the biomass of seagrass present (Table 4). There was no significant

difference in the biomass of seagrass between the 2 times of sampling (1 and 4 wk), nor was there an interaction between time and treatment, suggesting that the reduction in seagrass biomass in the grazed and grazing control plots occurred at, or soon after, the experiment started and there had been little in the way of recovery of seagrass over the month of the experiment. At Site B, after 4 wk, the biomass of seagrass was reduced by 55% in the grazed plots and 25% in the grazing control plots compared to the ungrazed plots. Again, all 3 treatments were significantly different from each other (Table 4).

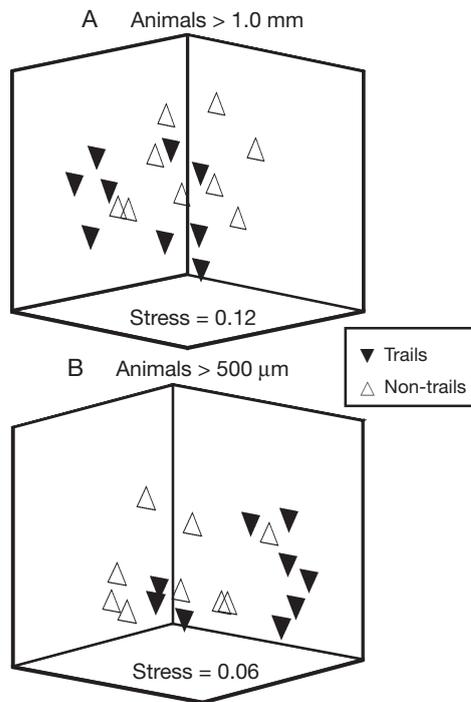


Fig. 2. nMDS ordinations (3-dimensional) on untransformed data for (A) animals >1 mm and (B) animals >500 µm, from cores taken within grazed areas (Trails) and nearby ungrazed areas (Non-trails). N = 3 replicates from each of 3 plots in the Trail and Non-trail areas

Table 3. ANOVAs on the biomass (grams DW) of seagrass in 4 m<sup>2</sup> plots from 3 different treatments (grazed, disturbance control, control) on 2 different occasions after simulated grazing (1 and 4 wk) at Site A and after 4 wk at Site B. Data were transformed to log<sub>e</sub>(x+1) to meet the assumption of homogeneity of variances

Source	df	MS	F	p
<b>Site A</b>				
Time	1	0.007	0.12	<0.75
Treatment	2	0.852	14.50	<0.001
Treatment × Time	2	0.060	1.02	<0.40
Plots (Treatment)	12	0.059	0.99	<0.48
Residual	36	0.059		
<b>Site B</b>				
Treatment	2	0.515	24.33	<0.003
Plots (Treatment)	5	0.021	0.49	<0.79
Residual	16	0.044		

Table 4. Post hoc SNK tests on the biomass (g, dry weight) of seagrass in 4 m<sup>2</sup> plots from 3 different treatments (grazed, disturbance control, control after simulated grazing). Data shown are means ± SE. Means with different letter in SNK column are significantly different from each other at p < 0.05

Treatment	Site A	SNK	Site B	SNK
Control	1.69 (± 0.15)	A	2.35 (± 0.23)	A
Disturbance	1.15 (± 0.14)	B	1.76 (± 0.21)	B
Grazed	0.23 (± 0.09)	C	1.06 (± 0.11)	C

Table 5. Summaries of ANOVAs on the abundance of different taxa in 4 m<sup>2</sup> plots from 3 different treatments (grazed, disturbance control, control) on 2 different occasions after simulated grazing (1 and 4 wk) at Site A and after 4 wk at Site B. N = 3 replicate cores from each of 3 plots on each occasion. Data were transformed to log<sub>e</sub>(x+1) where necessary to meet the assumptions of homoscedasticity after Cochran's test. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001, ns: not significant at p > 0.05, - : test for main effect inappropriate because of significant interaction term, na: insufficient animals in that taxon at that site to allow analysis

Variable	Site A Treatment	Site B T × Time	Treatment
Total no. individuals	***	ns	**
Gammarids	***	ns	*
Isopods	ns	ns	na
Tanaids	***	ns	**
Copepods	**	ns	*
Ostracods	-	*	**
Bivalves	*	ns	*
Gastropods	***	ns	**
Capitellids	*	ns	ns
Cirratulids	-	*	na
Nereidids	-	*	na
Opheliids	***	ns	*
Phyllodocids	na	na	ns
Sabellids	*	ns	ns
Spionids	ns	ns	ns
Syllids	-	**	*
Terebellids	***	ns	na
Nematodes	-	*	ns
Oligochaetes	ns	ns	ns

## Effects on benthic faunal assemblages—Site A

Responses by fauna at Site A to the experimental reduction in the biomass of seagrass and the associated disturbance to the seagrass and sediments varied among the different taxa present. There were 5 types of response: (1) significant effects of grazing but no effect of physical disturbance compared to the ungrazed control (Grazing < Grazing Control = Ungrazed); (2) significant effects of grazing disturbance but no additional effects of grazing (Grazing = Grazing Control < Ungrazed); (3) significant effects of grazing and grazing disturbance compared to ungrazed control (Grazing < Grazing Control < Ungrazed); (4) significant short-term (i.e. 1 wk) effects from grazing and disturbance, but these effects were not apparent at 4 wk; and (5) no effects from grazing or grazing disturbance.

## Significant effects of grazing but no grazing disturbance

Four taxa showed a significant decline in abundance (Table 5) in the plots where seagrass biomass was reduced by 86% (grazed), but there was no significant effect of the disturbance (grazing control), despite the removal of up to 32% of the seagrass from these plots. Gammarid amphipods (Fig. 3A) were reduced by 64%, gastropods (Fig. 3B) by 58%, capitellid polychaetes (Fig. 3C) by 48% and opheliid polychaetes by 67% (Fig. 3D) in the grazed plots compared to the ungrazed plots. The pattern of differences among the 3 treatments was consistent over time (no significant interaction between Time and Treatment, Table 5), and of these 4 taxa, only the opheliid polychaetes varied in abundance between the 2 times.

One taxon, the terebellid polychaetes (Fig. 3E), showed significant reductions in abundance in response to the experimental disturbance of the seagrass and sediments, but no additional effect in the grazed plots compared to the grazing control plots. This suggests that the disturbance to the substratum triggered the reduction in abundance for these animals. There was a trend for the lowest abundances to be in the grazed plots

(Fig. 3E). The interaction between Time and Treatment for terebellids (Table 3) was nearly significant ( $p < 0.08$ ). Examination of the data suggests that the abundance of these worms was smaller in the grazed plots than the ungrazed plots on both occasions, but the abundance in the grazing control plots was less than the ungrazed plots after 1 wk, but not after 4 wk.

## Significant effects of grazing and grazing disturbance

The total abundance of all animals (Fig. 4A) and the abundance of tanaid crustaceans (Fig. 4B) were significantly reduced by the disturbance to the substratum (grazing control plots), but in these cases

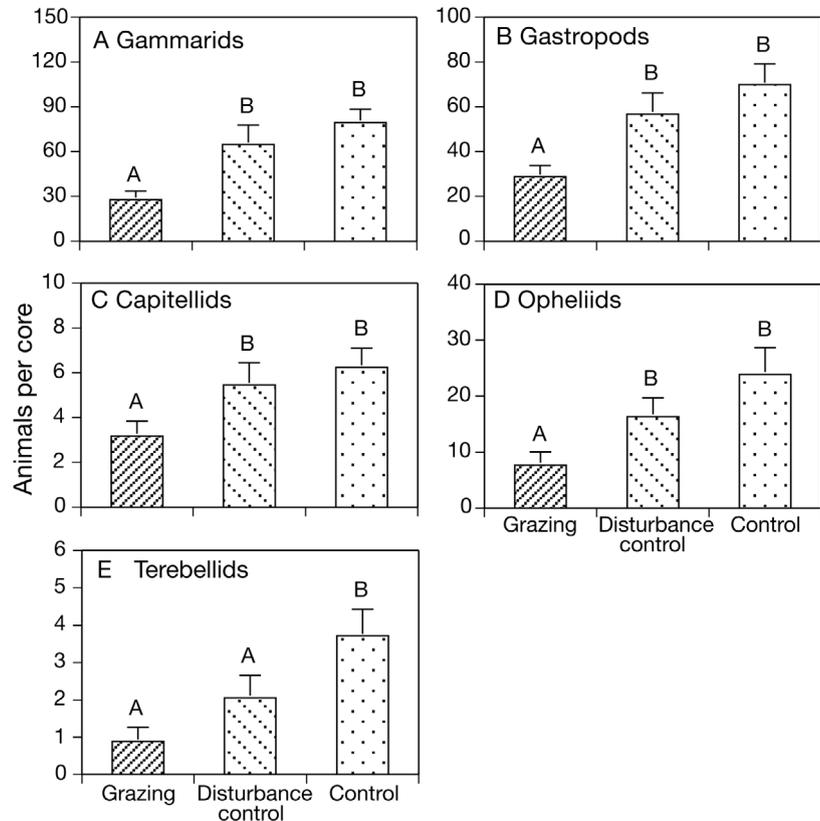


Fig. 3. Mean (+SE) number of (A) gammarid amphipods, (B) gastropods, (C) capitellid polychaetes, (D) opheliid polychaetes and (E) terebellid polychaetes (>500  $\mu\text{m}$ ) in the simulated dugong grazing experiment. A–D were significantly affected by the experimental reduction in seagrass biomass. E was significantly affected by the experimental disturbance in the seagrass and sediments. Three treatments were examined: 4 m<sup>2</sup> plots where the biomass of seagrass was reduced (Grazing), seagrass and sediments were disturbed (Disturbance Control) or unmanipulated (Control). N = 18 cores pooled across 3 plots  $\times$  2 times or each treatment. Data were transformed to  $\log_e(x+1)$  to stabilise variances after Cochran's tests. Means topped by different letters are significantly different from each other in post hoc SNK tests

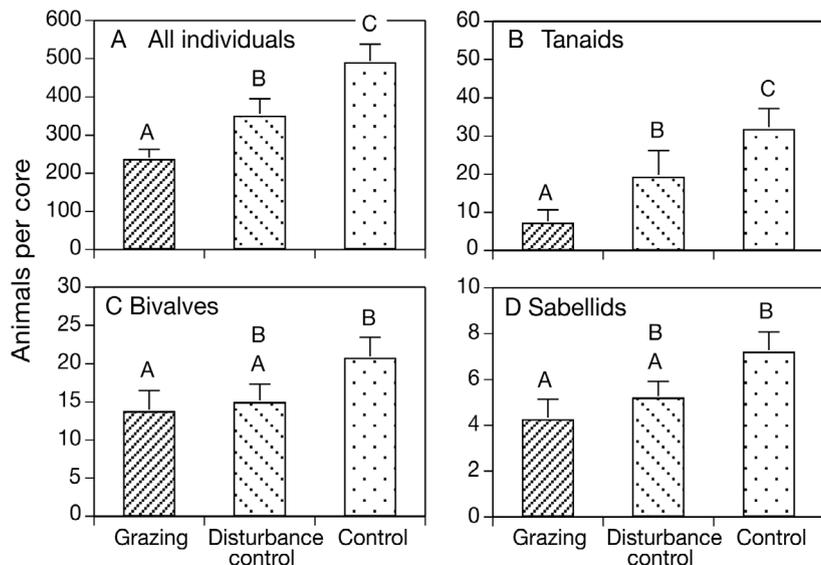


Fig. 4. Mean (+SE) number of (A) all individuals, (B) tanaids, (C) bivalves and (D) sabellid polychaetes (>500 μm). (A) and (B) were significantly affected by the experimental reduction of seagrass biomass and by the disturbance to seagrass and sediments. (C) and (D) showed a similar pattern, but post hoc tests could not clearly differentiate among the 3 treatments. Other details as in Fig. 3

there was an additional significant effect of seagrass removal in the grazed plots. Compared to the ungrazed plots, the abundance of all macrofauna and the abundance of tanaids in the grazing control plots was reduced by 28 and 39%, and in the grazed plots by 51 and 76%, respectively (Fig. 4A,B)

The abundance of 2 other taxa, bivalves (Fig. 4C) and sabellid polychaetes (Fig. 4D), was significantly reduced by the experimental treatments (Table 5), but post hoc comparisons were unable to distinguish among the specific treatments. In both cases, more animals were found in the ungrazed plots than in the other plots.

Significant short-term effects of grazing and grazing disturbance

Four different taxa showed significant short-term (1 wk) effects from the experimental treatments, but these effects were not evident after 4 wk (significant Time × Treatment interaction, Table 5). Ostracods (Fig. 5A) were significantly less abundant in the grazed and grazing control plots compared to the ungrazed plots after 1 wk, but there were no significant differences among the 3 treatments after 4 wk. In contrast, nereidid (Fig. 5B) and syllid polychaetes (Fig. 5C) were significantly less abundant in the grazed plots, but the grazing control and ungrazed plots did not differ from each other after 1 wk, although these effects had gone after 4 wk. Finally, the abundance of nemerteans (not shown) varied significantly among the 3 treatments, but the exact pattern of differences was unclear from the post hoc analyses. The important result here

is that however the impacts were manifested after 1 wk, these effects were no longer evident after 4 wk.

No effects of grazing or grazing disturbance

Two taxa, isopod crustaceans and spionid polychaetes, were apparently unaffected by the application of either experimental treatment (Table 5). There was some suggestion of a short-term (1 wk) effect of grazing and disturbance on the abundance of spionids, but if this trend was a result of the experimental treatments, then the effect was no longer evident after 4 wk.

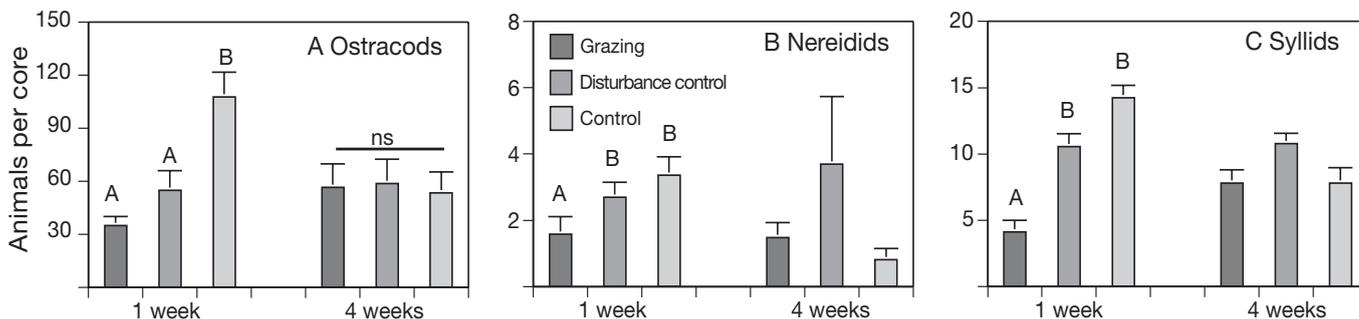


Fig. 5. Mean (+SE) number of (A) ostracods, (B) nereidid polychaetes and (C) syllid polychaetes (>500 μm). All showed significant, but variable, effects of grazing after 1 wk but these effects were no longer evident after 4 wk. ns: not significant. Other details as in Fig. 3

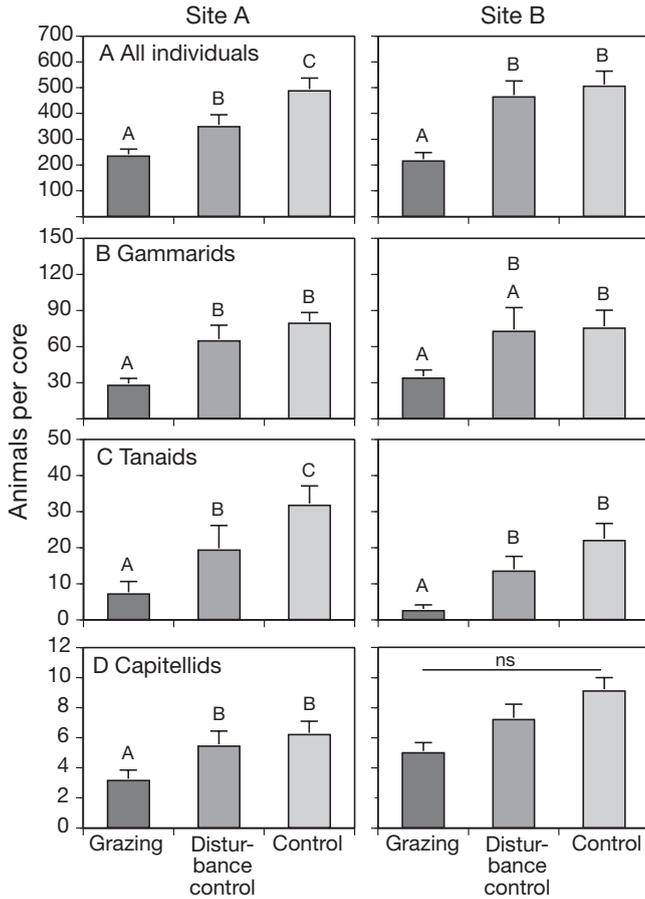


Fig. 6. Comparison of the effects of grazing after 4 wk potential recovery at Sites A and B for (A) all individuals, (B) gammarid amphipods, (C) tanaids and (D) capitellid polychaetes. For each taxon, the trend among treatments was similar, but the interpretation of the relative effects of grazing versus physical disturbance varied between the 2 sites. N = 9 cores pooled across 3 plots for each treatment. Data were transformed to  $\log_e(x+1)$  to stabilise variances after Cochran's tests. ns: not significant

**Generality of the results—Site A vs. Site B**

For the total number of individuals in the experimental plots, the trend among the treatments was similar at both sites (Fig. 6A), but interpretation of the relative effects of seagrass removal versus disturbance varied. At Site A, there was a significant effect of disturbance (grazing control plots) on the abundance of individuals, but there was a further reduction in abundance with the removal of greater amounts of seagrass biomass (grazing plots). In contrast, at Site B, there was a clear effect of the seagrass removal, but there was little effect from the experimental disturbance to the plots, despite the removal of significant amounts of seagrass as an indirect effect of this disturbance (Fig. 6A).

The pattern of differences among the treatments in the number of gammarid amphipods was also similar

at both Sites (Fig. 6B), but in this case, post hoc multiple comparisons (Student-Newman-Keuls [SNK] tests) were unable to distinguish among the treatments at Site B, whereas these tests had indicated a significant effect of seagrass removal at Site A. The reduced number of samples collected at Site B may have led to insufficient power to detect the differences among the treatments, given that the magnitude of these differences were similar at both sites. This conclusion is further supported by the analyses of the abundance of tanaid crustaceans (Fig. 6C) and the number of capitellid polychaetes (Fig. 6D).

At Site A, the abundance of tanaids was reduced by the effects of disturbance and further by the removal of seagrass in the simulated grazing treatments, whereas at Site B, only the effect of seagrass removal was found to significantly affect the abundance of tanaids. Seagrass removal significantly reduced the abundance of capitellid polychaetes (Fig. 6D) at Site A, but there were no significant differences among the treatments at Site B (Table 5) despite a similar trend among treatments.

The experimental treatments had very little effect on the abundance of ostracods at Site A, but caused a significant reduction in their numbers in the grazed plots at Site B compared to the ungrazed plots (Fig. 7A). A similar result was obtained for syllid polychaetes

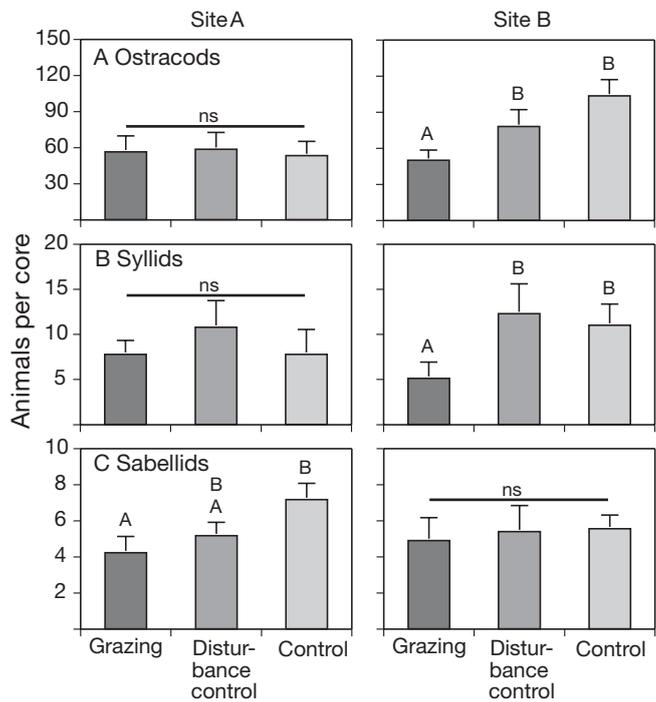


Fig. 7. Comparison of the effects of grazing after 4 wk potential recovery at Sites A and B for (A) ostracods, (B) syllid polychaetes and (C) sabellid polychaetes. ns: not significant. Other details as in Fig. 6

Table 6. Non-parametric multivariate analyses of variance (PERMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in plots from 3 different experimental treatments (grazed, disturbance control and control) at Site A, for 1 and 4 wk and Site B for 4 wk since application of the treatments. Data were unstandardised and 4th root transformed;  $n = 9$  cores pooled across 3 plots per treatment. Full model used for both sites

Source	df	MS	<i>F</i>	<i>p</i>	Possible no. permutations
<b>Site A</b>					
Time	1	1820.38	3.52	0.0002	$1.0 \times 10^{10}$
Treatment	2	2060.74	3.99	0.0002	$1.0 \times 10^{10}$
Time $\times$ Treatment	2	974.48	1.89	0.0018	$1.0 \times 10^{10}$
Residual	48	516.65			
Total	53				
<b>Site B</b>					
Treatment	2	1240.01	3.70	0.0002	$2.8 \times 10^6$
Residual	15	334.69			
Total	17				

(Fig. 7B). The opposite situation was evident for sabelid polychaetes (Fig. 7C). There was a significant effect of the experimental treatments on the abundance of sabelids at Site A, although the nature of these effects could not be distinguished, but at Site B there was no significant effect of the experimental treatments (Table 5).

#### Effects of grazing and grazing disturbance on community composition

The composition of the macrofaunal community at Site A was significantly affected by the application of the experimental treatments, but the differences among these treatments changed as time progressed (PERMANOVA, Table 6). Initially, after 1 wk, there were significant differences among all 3 treatments (Table 7), but after 4 wk only the plots where the seagrass biomass had been experimentally grazed were different from the other plots (Table 7). The results of the analyses on the data from Site B after 4 wk were similar to those obtained for Site A, with a significant effect of grazing but no effect of the grazing controls evident after 4 wk (Tables 6 & 7).

## DISCUSSION

Grazing by dugongs results in the removal of large amounts of seagrass and considerable disturbance to the substratum as the plants are uprooted (Preen 1995). Importantly, our results indicate that the physical disturbance from grazing also causes a significant decline in the biomass of the seagrass. Sediment that is

displaced during feeding forms mounds on either side of the feeding trail, potentially burying animals as it then slumps back into the trail from water movement. Additionally, during feeding, the finer particles are resuspended, eventually settling back onto the substratum at varying distances from the feeding trail dependent upon ambient water flow. These fine sediments may potentially then bury animals in and around the feeding trails, or animals attempting to colonise any remaining seagrass. Direct burial of organisms due to sedimentation is therefore a potential impact arising from dugong feeding.

Up to 85% fewer animals were present in dugong feeding trails compared to adjacent, ungrazed areas, although for individual taxa, the magnitude of the differences varied, and for some taxa, there was no effect of grazing on their abundance. Similarly, the overall composition of the benthic, infaunal assemblage in the grazed areas was different from that in the ungrazed areas. The groups of animals most affected by dugong grazing were small crustaceans and polychaetes, all of which are potentially important food for estuarine fish (e.g. Coull et al. 1995) and shorebirds (Zharikov & Skilleter 2003, 2004).

These significant impacts on benthic assemblages associated with seagrass occurred at the scale of an individual grazing dugong. However, these impacts

associated with seagrass occurred at the scale of an individual grazing dugong. However, these impacts

Table 7. Non-parametric, pair-wise post hoc comparisons after multivariate analyses of variance (PERMANOVA). Other details as in Table 6. (A) Pair-wise post hoc comparisons for interaction–Site A; (B) Pair-wise post-hoc comparisons for treatment effect–Site B (see Table 6 for results of PERMANOVA)

	<i>t</i> -value	<i>p</i>	Possible no. permutations
<b>Site A</b>			
1 wk			
Grazing vs Disturbance	1.36	0.0100	$2.43 \times 10^4$
Grazing vs Control	2.31	0.0002	$2.43 \times 10^4$
Disturbance vs Control	1.51	0.0098	$2.43 \times 10^4$
4 wk			
Grazing vs Disturbance	1.72	0.0006	$2.43 \times 10^4$
Grazing vs Control	2.03	0.0002	$2.43 \times 10^4$
Disturbance vs Control	1.07	0.2854	$2.43 \times 10^4$
<b>Site B</b>			
4 wk			
Grazing vs Disturbance	1.99	0.0048	462
Grazing vs Control	2.38	0.0024	462
Disturbance vs Control	1.11	0.2064	462

are likely to have far greater importance for local seagrass beds because of the number of dugongs grazing in Moreton Bay at any time. Between 850 and 1000 dugongs use Moreton Bay, and they are frequently seen associated with seagrass beds (Lanyon 2003). In fact, Lanyon (2003) reported that large herds frequent the same seagrass-covered banks within the bay, repeatedly grazing the same areas, and that densities of dugongs foraging on these seagrass beds are greater than have been reported elsewhere in Australia. Clearly, given the dependence of dugongs on seagrass for food, the magnitude of the impacts on associated benthic assemblages is likely to be considerable.

The total number of animals and the abundance of several individual taxa in the different plots was positively correlated with seagrass biomass, suggesting that the differences in the abundance of these animals in the grazed and ungrazed areas was a direct response to the removal of the seagrass or to some associated factor that was closely linked to the amount of vegetation present. Previous studies (e.g. Heck & Wetstone 1977, Lewis & Stoner 1983) have also found positive correlations between the abundance of benthic fauna and the biomass of seagrass, so this result was not surprising, although it does provide further support for the contention that the loss of the vegetation is a key component in the way disturbances affect the fauna in subtropical seagrass beds (Skilleter et al. 2006).

The abundance of some taxa, such as gammarid amphipods, was not correlated with the biomass of seagrass, despite the fact that there were significantly fewer animals in the grazed than ungrazed areas. This raises the possibility that amphipods were affected by some other factor associated with grazing, such as the substantial disturbance to the sediments that occurs. Many gammarids are closely associated with the vegetation (e.g. Stoner & Lewis 1985), but others are primarily infaunal (e.g. Ambrose 1984). More detailed identification of the different groups of amphipods in the samples would be required to determine their habitat-specificity, in combination with experimental manipulations of removal and/or disturbance (see below).

The abundance of groups such as bivalves was positively correlated with the biomass of seagrass in the plots, but was not different between the grazed and ungrazed areas, despite the fact there was considerably less seagrass in the grazed than ungrazed plots. Such a pattern would result if the biomass of the seagrass affected the abundance of the bivalves at settlement, but had little influence over their subsequent patterns of distribution. Thus, changes to the seagrass at some stage after settlement had no impact on the abundance of the bivalves. Passive trapping of larvae

by seagrass at different densities influences small-scale spatial variation in the distribution of infauna (e.g. Stoner & Lewis 1985, Peterson 1986) due to hydrodynamic baffling of water flow.

Previous studies on the effects of mega-herbivore grazing in seagrass beds have found variable effects on the macrofaunal communities. Macia (2000) found no effects on the invertebrate community from natural levels of grazing by urchins. In contrast, Rose et al. (1999) found that large densities of urchins removed greater than 95% of the seagrass biomass leading to significant declines in the abundance of both infaunal and epifaunal molluscs. In our study, grazing by dugongs resulted in significantly fewer animals in a range of different taxa, including gastropods, but there were no significant differences in the abundance of bivalves in grazed and ungrazed areas.

Gammarid amphipods, gastropods and 2 families of polychaetes (capitellids and opheliids) were significantly affected by the removal of the seagrass alone (i.e. no associated effect of the disturbance component). The abundance of amphipods is often highly correlated with both the biomass and surface area of seagrasses (Lewis & Stoner 1983, Stoner & Lewis 1985), possibly due to habitat selectivity in response to predation pressure (Orth et al. 1984). The abundance of terebellid polychaetes was significantly reduced by the grazing treatment, but this effect was attributable to the disturbance component, not to the removal of the vegetation. This group is closely associated with the sediment, so it is not surprising that the decline in abundance was a result of physical disturbance. A wide variety of different taxa is affected by disturbance to sediments, including different groups of polychaetes (Zajac & Whitlatch 1982).

There were some differences in the responses of the fauna at 4 wk, compared to those already present after 1 wk. Ostracods, nereidid and syllid polychaetes and nemerteans were all significantly affected by the simulated grazing after 1 wk, but these effects were no longer evident after 4 wk. These taxa are closely associated with the sediments rather than the vegetation. Presumably, displaced animals or other individuals migrated back into the plots after the initial period of disturbance. The other taxa were still significantly affected by either the loss of vegetation, the associated physical disturbance or both after 4 wk. Recovery of the seagrass in areas affected by physical disturbance often takes considerably longer than 4 wk, although some genera, including *Halophila* and *Halodule*, are able to recover within a few months of being disturbed (Fonseca et al. 1987, Duarte et al. 1997). Given that many of the taxa that were affected responded primarily to the loss of vegetation, recovery of these populations of animals to levels commensurate with ungrazed

reference areas would probably not occur until the vegetation had recovered.

A variety of studies has investigated grazing in terrestrial ecosystems by studying the effects of ungulates on associated animal communities in woodlands (Baines et al. 1994, Bromham et al. 1999) and grasslands (Abensperg-Traun 1992, Holt et al. 1996). The effect of grazing on animal communities is highly variable between animal groups and depends on the type and abundance of herbivores, their frequency of grazing and the ecosystem studied (Lubchenco & Gaines 1981). Deer grazing in pinewoods causes large decreases in the abundance of arthropods associated with the foliage (Baines et al. 1994). Similarly, cattle grazing in semi-arid pastures results in declines in populations of termites and mites (Holt et al. 1996). Small crustaceans were one of the primary groups affected by dugong grazing in our study. These significant declines in crustacean abundance were directly related to seagrass removal through grazing. In contrast, some other studies have shown that a high grazing disturbance causes increases in the abundance of ground-dwelling invertebrates (Bromham et al. 1999, Seymour & Dean 1999). However, this increase is due to the proliferation of a few disturbance-adapted species, at the expense of other species and the overall species diversity (Bromham et al. 1999, Seymour & Dean 1999).

The effects of grazing by mega-herbivores on animal communities in terrestrial systems are often highly variable, so any general conclusions from terrestrial grazing studies may not be applicable to aquatic ecosystems. The effects of grazing in aquatic habitats have not been studied as thoroughly as in terrestrial systems, yet the available data demonstrate that aquatic herbivores may also have a considerable impact on animal communities associated with grazed aquatic plants (Rose et al. 1999, this study). Populations of some aquatic macro- and mega-herbivores have the capacity to consume considerably more primary production than terrestrial grazers (Cebrian & Duarte 1994). At large densities, sea urchins affect both seagrass and associated faunal communities (Rose et al. 1999, Macia 2000). At normal sea urchin density (up to 10 m<sup>-2</sup>), grazing has no effect on benthic invertebrates (Macia 2000); however, overgrazing caused by urchin outbreaks (364 ind. m<sup>-2</sup>) causes significant declines in assemblages of molluscs associated with the seagrass (Rose et al. 1999). Aquatic herbivores therefore have the potential to significantly alter animal communities associated with seagrass habitats; clearly, mega-herbivores such as dugongs show this capacity.

The effect of dugong grazing on fauna associated with seagrass has not been previously investigated. As noted above, grazing by individual dugongs causes

large and measurable disturbances to localised seagrass patches. Further, dugong herds, as occur in some areas such as Moreton Bay, cause regular large-scale disturbances to seagrass meadows. The intensity of these grazing disturbances is sustained over periods of weeks to months and is repeated at intervals as dugongs re-graze areas (Preen 1995, Lanyon 2003). This contrasts with the impacts of sea urchins, which only occasionally occur in large enough densities to have significant effects on seagrass communities (Rose et al. 1999). Therefore, the magnitude of the effects of grazing on fauna by herds of dugongs is likely to be quite different from that of urchins. However, grazing by dugongs is somewhat similar to grazing by terrestrial herbivores and over-grazing by urchins, in that it causes a decline in the abundance of animals associated with the grazed habitat, but this was mostly associated with the disturbance of the sediment during dugong grazing rather than seagrass removal. Likewise, terrestrial studies have identified 2 main effects of ungulate grazing: removal of the plant material and compaction of the sediment (Holt et al. 1996, Bromham et al. 1999). In terrestrial ecosystems, however, plant removal and the reduction in plant biomass is believed to be the major factor in regulating faunal communities through grazing (Baines et al. 1994). Dugongs have an effect on fauna that is quite distinct from that of terrestrial and other aquatic herbivores, in that both sediment disturbance and removal of the plant material have a significant impact on different faunal constituents. Therefore, dugongs play a unique ecological role in structuring seagrass and associated animal communities.

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