

Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing

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ABSTRACT: In Moreton Bay, Australia, dugongs (*Dugong dugon*) often graze in large herds at the same location for weeks to months. Such grazing reduced seagrass shoot density by 65 to 95 %, above-ground biomass by 73 to 96 % and belowground biomass by 31 to 71 % at 3 sites ranging in size from 2 to 75 ha. Following even the most intense and sustained grazing, the space between surviving tufts of seagrass remains small (<1 m²) and recovery is usually rapid (months). In this regard, intensive grazing differs from disturbances caused by storms, sedimentation or disease. However, recovery of seagrass meadows can be suppressed by low levels of sustained grazing pressure. The species composition of seagrass meadows can be altered by intensive grazing, which favours rapidly growing, early pioneer species, such as *Halophila ovalis*, at the expense of slower growing but dominant species such as *Zostera capricorni*. In Moreton Bay, *H. ovalis* is the most nutritious (high nitrogen, low fibre) and the most preferred seagrass grazed by dugongs. *Z. capricorni* is the least preferred species. By preventing the expansion of *Z. capricorni* and increasing the abundance of *H. ovalis*, this grazing system, termed cultivation grazing, can improve the quality of the dugong's diet.

KEY WORDS: Cultivation grazing · Seagrasses · Dugongs

INTRODUCTION

Dugongs (*Dugong dugon*) are large marine mammalian grazers of the tropical Indo-west Pacific region, where they feed primarily on near-shore seagrasses (Lipkin 1975, Johnstone & Hudson 1981, Marsh et al. 1982). Nutritionally, many herbivores are constrained by the limited abundance of dietary nitrogen (Sinclair 1977, Mattson 1980, White 1993), and seagrasses have low levels of nitrogen compared with terrestrial grasses (Birch 1975, Duarte 1990, Lanyon 1991). Dugongs are further constrained by their rudimentary dentition, which leaves them ill-equipped to process fibrous plant material (Lanyon 1991). In Moreton Bay, at the southern limit of their range in eastern Australia, dugongs counter these constraints by feeding on soft-bodied invertebrates (Preen 1995) and by feeding selectively to maximise their intake of preferred (high

nitrogen, low fibre) seagrasses (Preen 1993). They feed primarily in communities dominated by their preferred early pioneer species, and on patches of such species within other communities (Preen 1993). During most of the year, dugongs avoid grazing communities dominated by the relatively fibrous *Zostera capricorni* (broad-leafed morph), which is the dominant species in the area (Preen 1993). However, where *Z. capricorni* is intermingled with more preferred species, it is consumed (Preen 1993). Dugongs are generally prevented from feeding selectively at the individual plant level by their wide muzzles (22 cm; Spain & Heinsohn 1975) and by their habit of cropping along serpentine feeding paths, known as feeding trails (see Fig. 1b).

In Moreton Bay, where there is no significant grazing of seagrasses by fish, birds or invertebrates, and where there appears to be relatively low grazing pressure from green turtles *Chelonia mydas*, dugongs are the main consumers of seagrasses. They usually feed in large herds (median herd size 140), which often graze the same location for periods of up to a month or more

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(Preen 1993). Such grazing may have a profound impact on the seagrasses. In this paper, I examine the ecological effects of this grazing on seagrass communities by documenting the grazing and recovery of heavily cropped areas, and by describing a manipulative experiment that simulated dugong grazing in a mixed seagrass community. I conclude that cultivation grazing maximises the abundance of seagrass species that are preferred by dugongs, at the expense of less preferred species. This grazing pattern appears to be a deliberate strategy to improve the quality of the dugong's diet.

METHODS

Study area. The study area was located in the east of Moreton Bay, a 1400 km², wedge-shaped embayment located in subtropical Queensland, on the east Australian coast (27.5° S, 153.3° E). Moreton Bay is approximately 100 km long and ranges in width from 1 km in the south to 31 km in the north. The study area encompassed a quartz sand delta that fans westwards between Moreton and North Stradbroke Islands, which form the seaward side of the bay. The study area contains 110 km² of predominantly subtidal seagrass meadows (to a maximum depth of 7 m) and supports approximately 600 dugongs (Preen 1993).

Grazing and recovery of feeding areas. Grazing sites were identified during regular, standardised aerial surveys (detailed in Preen 1993), or during boat-based encounters with dugong herds. The most reliable counts of grazing dugongs were made during the aerial surveys. It was difficult to locate and sample feeding areas before they had been substantially disturbed because the dugongs' mobility made it impossible to predict their movements between aerial surveys (approximately 3 wk apart) and the large size of many feeding herds meant that substantial disturbance could occur quickly. Consequently, I speculatively sampled many sites to assess the abundance of seagrasses before significant grazing occurred. As I did not expect many of these sites to be substantially grazed, it was not practical to sample them exhaustively. I measured the abundance of seagrass prior to, and following, intensive grazing at 3 areas, and I monitored the recovery of 2 of these. I also followed the succession of species at a fourth area that apparently had been grazed previously. The size of sampling quadrats varied, depending on the density and uniformity of the seagrasses. The size of grazed areas was measured from digitised vertical aerial photographs that were used to map the seagrass communities.

Area 1: This area had a uniform cover of the following seagrasses (in decreasing order of abundance):

Halophila ovalis, *Halophila spinulosa*, *Halodule uninervis* (broad-leafed morph; >1 mm wide) and *Zostera capricorni* (broad-leafed morph; >1 mm wide). Pre-grazing seagrass abundance was measured on the day grazing commenced (9 January 1990) by counting shoots in 18 quadrats (each 0.008 m²) haphazardly located around the dugongs' first feeding trails. Post-grazing seagrass abundance was assessed 12 d later using 110 haphazardly located quadrats (each 0.005 m²).

Area 2: This area was characterised by 1 to 20 m diameter patches of *Zostera capricorni* (broad) scattered through a matrix of *Halodule uninervis* (broad). Grazing was restricted almost exclusively to the *H. uninervis*. Grazing commenced in mid-August 1989, and generally extended northwards until the end of November. Pregrazing seagrass abundance (shoot density and biomass) of *H. uninervis* was determined on 22 November from 10 quadrats (0.005 m²) haphazardly located in ungrazed clumps of seagrass adjacent to feeding trails. Postgrazing recovery was monitored over 5 mo using 3 permanent, 20 m transects located 200 to 400 m apart in the *H. uninervis*. The seagrass was sampled in 10 quadrats (0.05 m²) along each transect at 2 to 3 mo intervals (22 November 1989, 21 January 1990 and 1 May 1990). The direction of sampling along the transects, and the side of the transect sampled were varied to ensure that quadrats sampled different locations in each sampling period. Quadrats were excavated to a depth of 5 to 10 cm and processed in the laboratory to determine shoot density and dry-weight biomass.

Area 3: This area encompassed an almost monospecific stand of *Halophila ovalis* (Fig. 1a), with a trace of *Halodule uninervis* (narrow-leafed morph; ≤1 mm wide). Aerial and boat-based surveys established that grazing commenced on or about 6 March 1989 and continued until 23 March. Pregrazing abundance of seagrass was assessed on 8 March by counting shoots in 17 quadrats (0.023 m²) haphazardly located around some recent feeding trails (Fig. 1b). The recovery of the seagrass community was monitored for over 9 mo using 3 × 20 m transects, like those used at Area 2, that were 150 m apart. Ten quadrats (0.05 m²) were sampled along each transect on 6 occasions between 23 March 1989 and 7 January 1990. Quadrats were excavated and processed in the laboratory. The area was intensively grazed a second time during the period of monitoring, on 4 September 1989. These 2 grazing incidents at Area 3 are referred to as 3-1 and 3-2.

It was not feasible to establish specific control sites adjacent to each grazing area, due to the likelihood that grazing would eventually extend into those sites. To locate control sites far from the grazing areas would be of questionable validity due to changes in species

composition, water depth and other variables. I used an alternative approach to gain an indication of the recovery of the grazed areas to their predisturbance states. I determined the seasonal growth patterns of the seagrasses by monitoring 9 sites throughout the study area at intervals of 3 mo for 2 yr ($25 \times 0.005 \text{ m}^2$ quadrats site^{-1} sampling period $^{-1}$). As these sites were not protected with exclosures, they may have experienced some low-intensity grazing on some occasions during the 2 yr. If they did, it was not obvious, and it was unlikely to have affected the seasonal growth patterns. Between seasons of minimum and maximum abundance, the shoot density, above- and below-ground biomass varied by factors of 1.2, 2.4 and 1.6, respectively, for *Halodule uninervis* and by 2.2, 1.9 and 2.7 for *Halophila ovalis* (Preen 1993). I used the seasonal growth data to develop correction factors which I applied to the pregrazing abundance of seagrass at grazing Areas 2 and 3 to predict how those seagrass meadows may have changed through the seasons, had no grazing occurred. Comparisons between the abundance of seagrass at the grazed areas and the predicted changes provide an indication of the areas' recovery.

Area 4: When first sampled, this site had a low biomass cover of *Halophila ovalis* and *Halophila spinulosa*. The sediments, however, contained a large amount of dead rhizome of *Zostera capricorni* (broad). Based on the decomposition rate of *Zostera* rhizomes (Kenworthy & Thayer 1984, Preen 1993) it is apparent that *Z. capricorni* was a conspicuous species at this site 3 to 6 mo prior to sampling. The Maroom Bank, on which this site was located, is dominated by *H. spinulosa* and *H. ovalis*, with *Z. capricorni* intermingled in patches. As this area was a favoured dugong grazing area during this study (Preen 1993), it was likely that the low seagrass biomass and absence of *Z. capricorni* at Area 4 was due to intensive grazing. Hence, the seagrasses at this site were monitored for the subsequent 2 yr. At 3 mo intervals, from July 1988 to April 1990, 25 quadrats (each 0.05 m^2) were sampled from along a permanent 50 m transect. Quadrats were placed at 2 m intervals along the transect, which was sampled from different directions and on different sides during each sampling period to prevent resampling of the same quadrat sites. Quadrats were excavated and processed in the laboratory to determine shoot density and biomass.

Exclosure experiment. A manipulative experiment that simulated dugong grazing was established in the seagrasses on the Maroom Bank to test the following hypotheses: (1) that the expansion of *Zostera capricorni* on the Maroom Bank is not restricted by a physiological limitation; (2) that low-intensity grazing by dugongs does not change the relative abundance of

species in the seagrass meadow; (3) that intense grazing by dugongs does not retard the expansion of *Z. capricorni* or encourage the dominance of *Halophila ovalis*.

Exclosures were used to protect plots of the following 3 simulated grazing treatments from the confounding influences of uncontrolled grazing by dugongs: (1) No-grazing: exclosure only. The seagrass was not disturbed. (2) Low-intensity grazing: 3 simulated feeding trails that were 3 m long, 18 cm wide, approximately 6 cm deep and 1 m apart. The 'trails' were excavated using a garden spade and closely resembled natural feeding trails in terms of shoot density and patchiness. (3) High-intensity grazing: intensive grazing was simulated by removing most of the seagrass from a 9 m^2 area. Shoots and rhizomes were removed by hand until the shoot density and patchiness of the seagrasses resembled a heavily grazed meadow (90 to 95 % seagrass removal; see below).

A plot of each grazing treatment was established at each of 3 replicate, subtidal sites. The sites were approximately 2.5 m below mean sea level and were at least 2 km apart. A fourth site was used to examine the effect of the exclosures on seagrass abundance; seagrasses were monitored within an exclosure and within an equivalent unprotected plot (no exclosure) about 2 m away. The control site was not located with the treatment sites because of the likelihood that unprotected plots would be grazed. Instead, the control site was located in the same seagrass community in an area not used by dugongs (presumably because of greater boat traffic). The limited availability of this seagrass community in areas not used by dugongs prevented the replication of exclosure-control sites.

The experimental seagrass community contained approximately equal proportions of *Zostera capricorni* (broad), *Halophila spinulosa* and *Halophila ovalis*. This mix was chosen as it was similar to a previously studied feeding site where *Z. capricorni* was grazed when interspersed with *H. spinulosa* and *H. ovalis*. *Z. capricorni* was usually avoided when it occurred at higher densities (Preen 1993).

The $3 \times 3 \text{ m}$ exclosures consisted of wooden stakes projecting 25 cm above the sediment and linked by light (4 mm) rope around the perimeter and across the top. Hence, they formed a 25 cm high fence around the enclosed area with an open net (1 m^2 mesh) over the top. They were designed to deter dugong and turtle grazing without affecting light and water-flow regimes. The exclosures would not stop a determined dugong from feeding through the top mesh, but it was hoped that the fence would interrupt a dugong's feeding motion and so prevent feeding trails from crossing the experimental areas. The use of the area by boats precluded the construction of higher fences that could

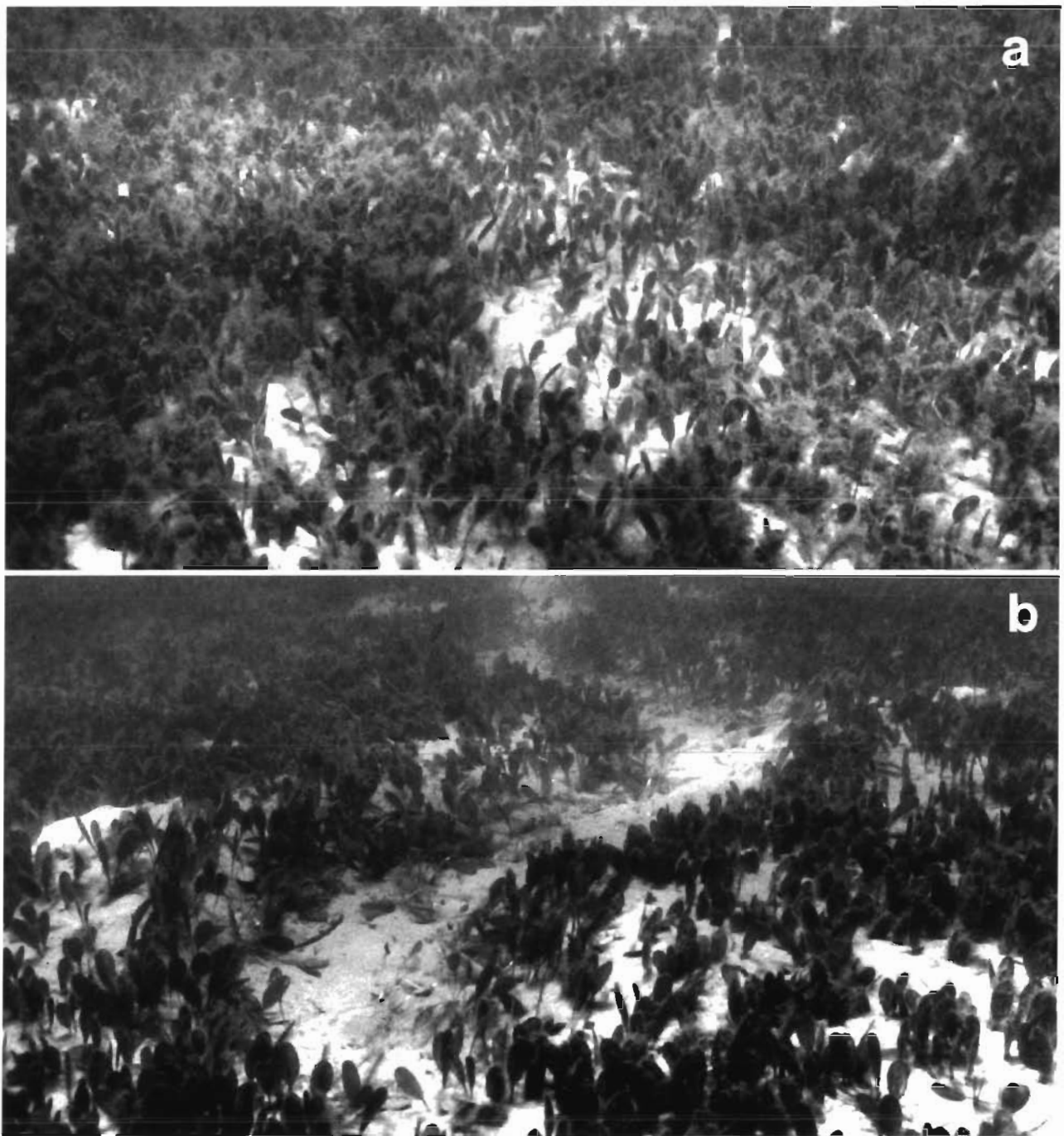


Fig. 1. (Above and facing page.) Impact of dugong grazing at Area 3-1. (a) Ungrazed tract of *Halophila ovalis*. (b) A single feeding trail at the same location. (c) Same location after 3 h grazing by about 70 dugongs. As many as 459 dugongs grazed this area for about 17 d, reducing the density of seagrass shoots by 95% over an area of 41 ha. Seagrass leaves are approximately 35 mm tall

have excluded herbivores. The unprotected site was marked with 4 corner pegs that projected 1 cm above the sediment.

To minimise the influence of very small-scale patchiness in the seagrasses, the abundance of seagrass was

monitored over an area of 4 m² within each 9 m² enclosure. These core areas were surrounded by a 0.5 m wide buffer, to avoid any edge effect. The ropes of the enclosures were cleaned of drift algae at intervals of 1 to 4 wk.



Seagrass shoots were counted in 0.023 m^2 quadrats systematically located in each enclosure. Thirty quadrats (6 quadrats along each of 5 transects) were monitored within each enclosure (and the unprotected plot), except in the low-intensity grazing treatment. In that treatment, 18 quadrats were monitored: 6 quadrats along each of the 3 simulated feeding trails. A pilot study indicated that at least 14 quadrats would be required to detect a 50% change in abundance. The position of each quadrat was rigidly controlled so repeat counts censused the same locations (± 2 to 5 cm). The abundance of seagrasses in the low- and high-intensity treatments was measured immediately prior to the seagrass manipulations. The abundance of seagrasses at all sites was then monitored on 4 occasions (approximately 100 d apart) between late June 1989 and early May 1990.

Statistical analysis: Shoot density [transformed by $\log_{10}(\text{shoot density} + 1)$ to equalise variances over the wide range of shoot densities] was analysed using a mixed-model analysis of variance. The response variable was the mean shoot density for each plot at each time ($n = 36$). Factors included in the model were species, grazing level, time and site. Site was taken as a random factor, while species, grazing level and time were fixed. The mixed model is thus a univariate repeated-measures model with 2 repeated factors (species and time). This model assumes a constant covariance structure over species, time and the species by time interaction. This was tested with the sphericity test (SAS Institute Inc. 1991) for species and time, but it

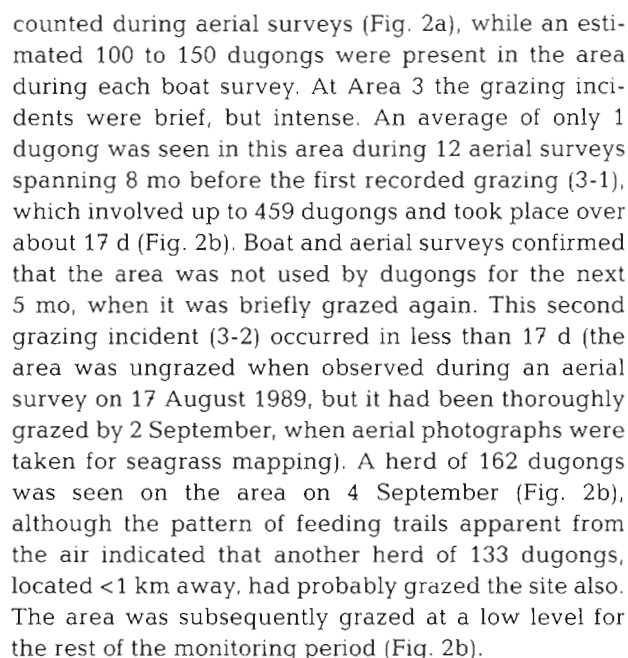
was not possible to test the interaction due to the limited degrees of freedom. The model also assumes that there was no interaction between site and grazing treatment. This is a reasonable assumption given that the sites were carefully selected for their similarity of species composition, shoot density, sediment type and water depth. Residual plots were used to assess the data for homoscedasticity of variances.

RESULTS

Grazing and recovery of feeding areas

Number of grazing dugongs

Like other large herbivores (Leuthold 1977), dugongs appear to spend most of their time grazing. Hence, the density of dugongs on a seagrass meadow during the day provides an indication of the intensity of grazing at that location. The number of dugongs that grazed Area 1 is unknown, although I estimated (from a boat) that approximately 50 dugongs were feeding at the site when it was first sampled. The dugongs had apparently left the area when it was resampled 12 d later. Between 60 and 219 dugongs were seen feeding in Area 2 on 8 consecutive aerial surveys over 4 mo (Fig. 2a). Most grazing around the monitoring transects occurred during the first month. During this period the area was searched 3 times from the air and 3 times from a boat. Herds of 153, 187 and 219 dugongs were



Amount of seagrass removed

At Area 2, shoot density, aboveground biomass and belowground biomass were reduced by 65, 73 and 31% respectively over 3.5 mo (Table 1, Fig. 3). Grazing

Fig. 2. Number of dugongs counted in (a) Area 2 and (b) Area 3 during aerial surveys. Shading indicates a second herd, of 133 dugongs, adjacent to and suspected of also grazing Area 3 on or before 4 September 1989. Insignificant numbers of dugongs were seen in these areas during 11 surveys preceding those graphed

Table 1. Abundance of *Halophila ovalis*, *Halophila spinulosa*, *Halodule uninervis* and *Zostera capricorni* at feeding areas before and after they were intensively grazed by dugongs, and the percentage of seagrass removed. 3-1 and 3-2 refer to the first and second grazing of Area 3. Biomasses are dry weights

	Area	Species	Seagrass abundance (mean \pm SE)		Reduction (%)
			Before grazing	After grazing	
Shoot density (shoots m ⁻²)	Area 1	All	1587.3 \pm 116.7	213.3 \pm 37.2	86.6
		<i>H. ovalis</i>	980.4 \pm 103.3	115.3 \pm 20.6	88.2
		<i>H. spinulosa</i>	504.2 \pm 74.1	76.9 \pm 21.9	85.8
		<i>H. uninervis</i>	66.7 \pm 32.5	3.8 \pm 2.7	94.2
		<i>Z. capricorni</i>	0.0	17.3 \pm 3.6	
		<i>H. uninervis</i>	2875.3 \pm 678.3	1016.4 \pm 157.3	64.7
	Area 3-1	<i>H. ovalis</i>	2839.2 \pm 133.5	155.9 \pm 30.6	94.5
	Area 3-2	<i>H. ovalis</i>	1445.7 \pm 110.4	118.3 \pm 22.0	91.8
Aboveground biomass (g m ⁻²)	Area 2	<i>H. uninervis</i>	16.9 \pm 4.7	4.6 \pm 0.8	73.0
	Area 3-2	<i>H. ovalis</i>	22.6 \pm 2.2	1.0 \pm 0.2	95.8
Belowground biomass (g m ⁻²)	Area 2	<i>H. uninervis</i>	137.6 \pm 13.9	94.8 \pm 11.5	31.1
	Area 3-2	<i>H. ovalis</i>	27.9 \pm 2.5	8.0 \pm 1.1	71.3

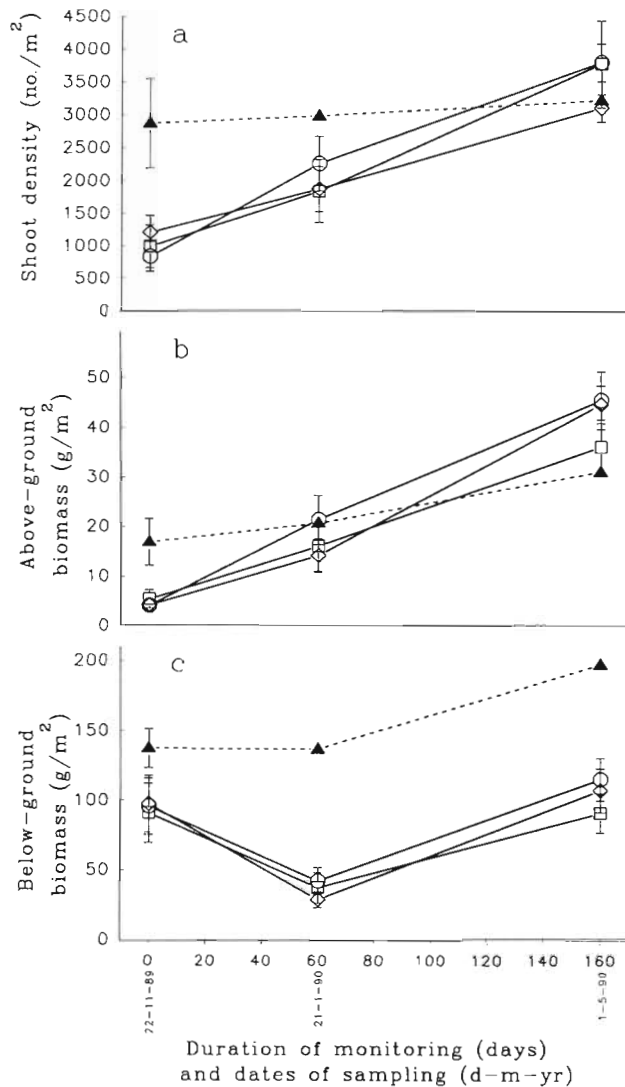


Fig. 3. *Halodule uninervis*. Response to intensive grazing by dugongs at Area 2. (a) Shoot density. (b) Aboveground biomass. (c) Belowground biomass. (□, ○, ◇) Seagrass abundance along 3 transects (\pm SE). Abundance of seagrass prior to grazing (\blacktriangle) has been seasonally adjusted to show the expected changes in the absence of grazing

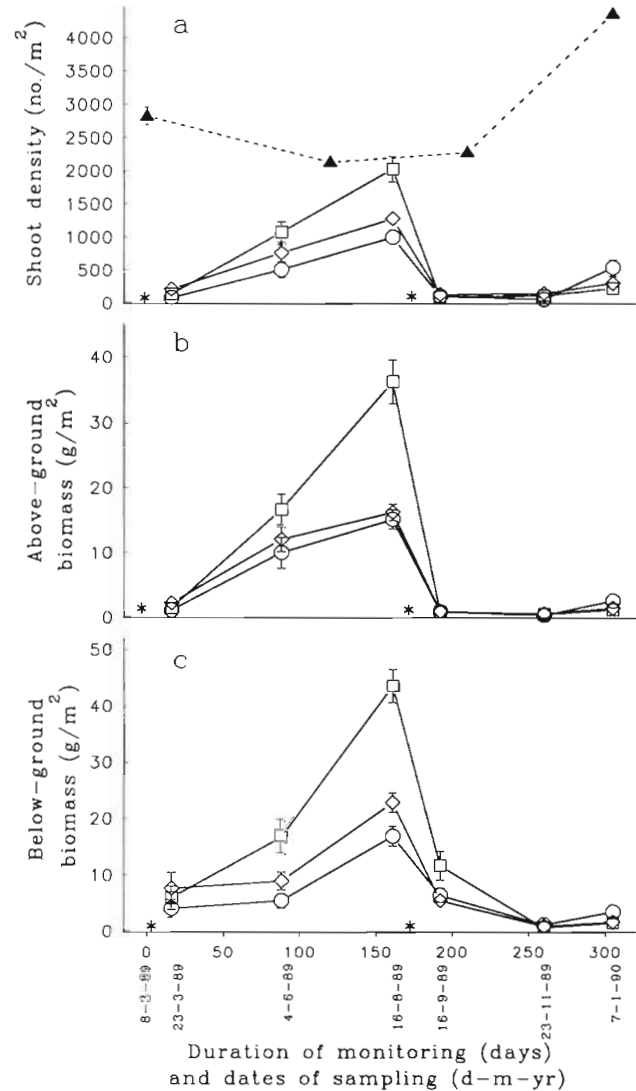


Fig. 4. *Halophila ovalis*. Response to intensive grazing by dugongs at Area 3. (a) Shoot density. (b) Above-ground biomass. (c) Below-ground biomass. (□, ○, ◇) Seagrass abundance along 3 transects (\pm SE). Abundance of seagrass prior to grazing (\blacktriangle) has been seasonally adjusted to show the expected changes in the absence of grazing. (*) Timing of the first and second grazing incidents

was more intensive at Areas 1, 3-1 and 3-2, where, respectively, the number of seagrass shoots was reduced by 87 % in 12 d, 95 % in about 17 d, and 92 % in less than 17 d (Table 1, Fig. 4). At Area 3-2 the biomass of seagrass was reduced by 96 and 71 % for the above- and belowground components respectively (Table 1).

These reductions represent the removal of large amounts of seagrass because large areas were affected: 2, 75 and 41 ha at Areas 1, 2 and 3, respectively. Based on the biomass of seagrass at Area 3 before and after the second grazing incident (Table 1),

and assuming that the 3 sampling transects were representative of the 41 ha area (as suggested by subsequent mapping; Preen 1993), I estimate that the dugongs consumed over 151 000 kg wet weight of seagrass in under 17 d.

Immediately following the second grazing incident at Area 3, the aboveground biomass had been reduced to 1.0 g m⁻² (SE 0.2) and the belowground biomass to 8.0 g m⁻² (SE 1.1; Table 1, Fig. 4). Despite the greatly diminished biomass of seagrass, dugongs continued to graze the area at a low intensity (Fig. 2b). By the end of November, when the seagrasses

were next sampled, this continued, low-intensity grazing had reduced the biomass of rhizomes and roots to 1.03 g m^{-2} (SE 0.19; Fig. 4). Compared with the level prior to the second grazing, this was a net reduction of 96.3%. The low-intensity grazing had little impact on the density or biomass of shoots [further reducing aboveground biomass to 0.56 g m^{-2} (SE 0.11) and changing shoot density from $118.26 \text{ shoots m}^{-2}$ (SE 22.02) to $112.41 \text{ shoots m}^{-2}$ (SE 23.32); Fig. 4].

Recovery

At Area 2, the shoot density and aboveground biomass of *Halodule uninervis* recovered to seasonally

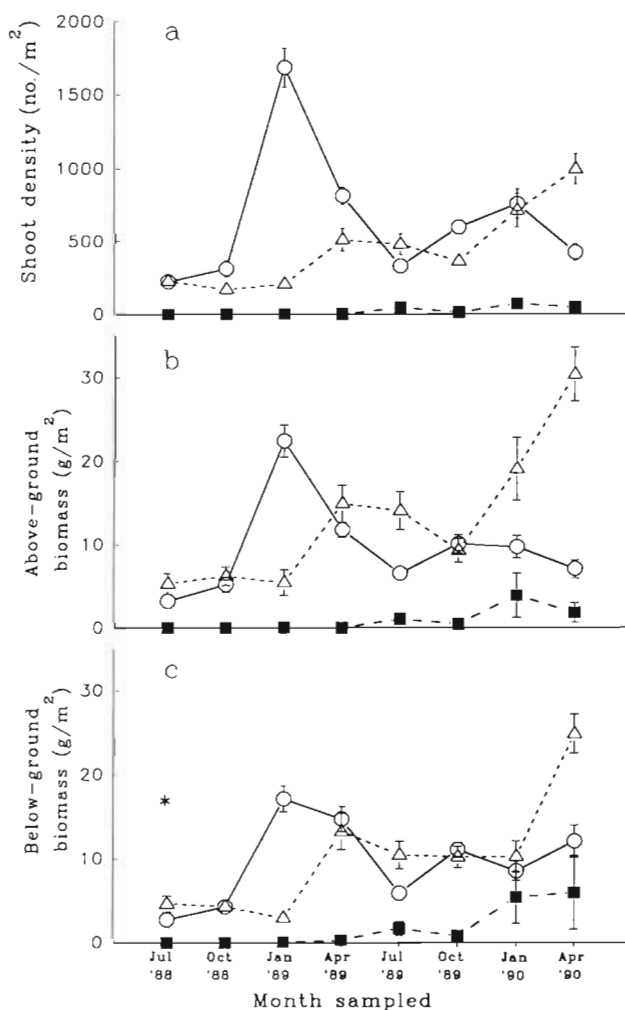


Fig. 5. Abundance (mean \pm SE) of (O) *Halophila ovalis*, (Δ) *Halophila spinulosa* and (\square) *Zostera capricorni* at Area 4 over 21 mo. (a) Shoot density. (b) Aboveground biomass. (c) Below-ground biomass. (*) Abundance of dead rhizomes of *Z. capricorni*.

adjusted pregrazing levels within 160 d, which spanned the summer and autumn growing season (Fig. 3a, b). The grazing may have stimulated an increase in the abundance of shoots above the level that would have been achieved in the absence of grazing (Fig. 3a). The belowground biomass, however, was much slower to recover, largely because it continued to decline after the grazing had finished (Fig. 3c). This response may have resulted from the eventual death of some small sections of rhizome created by the high density of intersecting feeding trails.

At Area 3, the initial recovery of the seagrass was rapid, despite the severity of the grazing (Fig. 4). Approximately 150 d after the first grazing, the average density of *Halophila ovalis* had increased 9-fold, from a postgrazing density of 156 (SE 31) to 1446 (SE 110) shoots m^{-2} . This represented a recovery to more than half (65%) of its seasonally adjusted, pregrazing abundance ($2215 \text{ shoots m}^{-2}$; Fig. 4). This recovery was achieved during autumn and winter, when the growth rate of *H. ovalis* is at its lowest (Preen 1993).

The second grazing event at Area 3 (3-2) removed 92% of the shoots of the recovering meadow of *Halophila ovalis* (Table 1). Despite a favourable growing period (spring–summer), continued low-level grazing by dugongs was enough to prevent any recovery within the next 100 d (Fig. 4).

The amount of seagrass at Area 4 increased during the 21 mo monitoring period. No major grazing events occurred during this time, although occasional low-level grazing was probably common. The relative and absolute abundance of *Halophila ovalis* increased rapidly soon after the monitoring commenced, and this species dominated the meadow for 6 mo (Fig. 5). *H. ovalis* was codominant with *Halophila spinulosa* for the next 6 mo, when *H. spinulosa* became the dominant species. Live *Zostera capricorni* first appeared at the site 9 mo after the monitoring commenced, presumably as a result of seed germination, and its abundance steadily increased through time (Fig. 5).

Exclosure experiment

Effect of exclosures

The exclosure had no effect on the abundance of *Zostera capricorni* or *Halophila spinulosa* (Fig. 6). The exclosure may have had a negative effect on the growth of *Halophila ovalis*, although this could not be confirmed without replication. This species displayed a summer peak in abundance in the unprotected plot, but not in the adjacent exclosure (Fig. 6). This response may have been due to shading by drift algae that accumulated on the exclosure ropes.

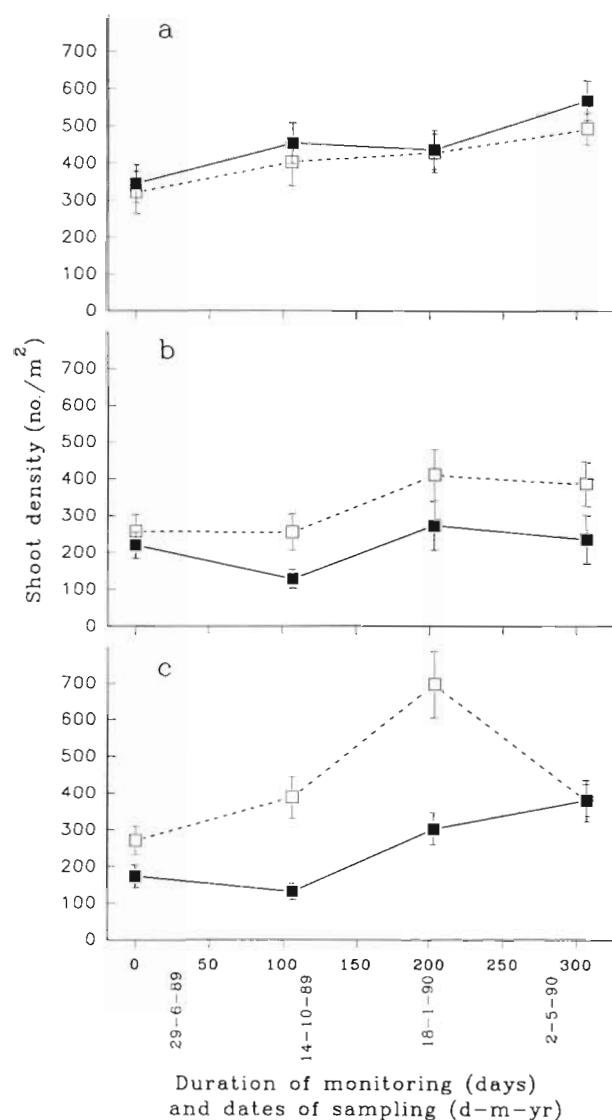


Fig. 6. Shoot density (mean \pm SE) of seagrasses in the (■) enclosure and the adjacent (□) unprotected plot at the enclosure control site. (a) *Zostera capricorni*, (b) *Halophila spinulosa*, (c) *Halophila ovalis*

Effects of grazing treatments

As expected, there were significant effects of grazing level, time and grazing level \times time (Table 2). The result of interest is the significant interaction between grazing level \times species \times time. To interpret this result, the means of each grazing level \times species \times time combination have been plotted, along with the critical values for Least Significant Difference comparisons (Fig. 7). Pretreatment shoot densities (for low- and high-intensity grazing treatments) have also been plotted, although these were not included in the analysis.

No-grazing treatment: In the absence of any grazing disturbance, the abundance of *Zostera capricorni*

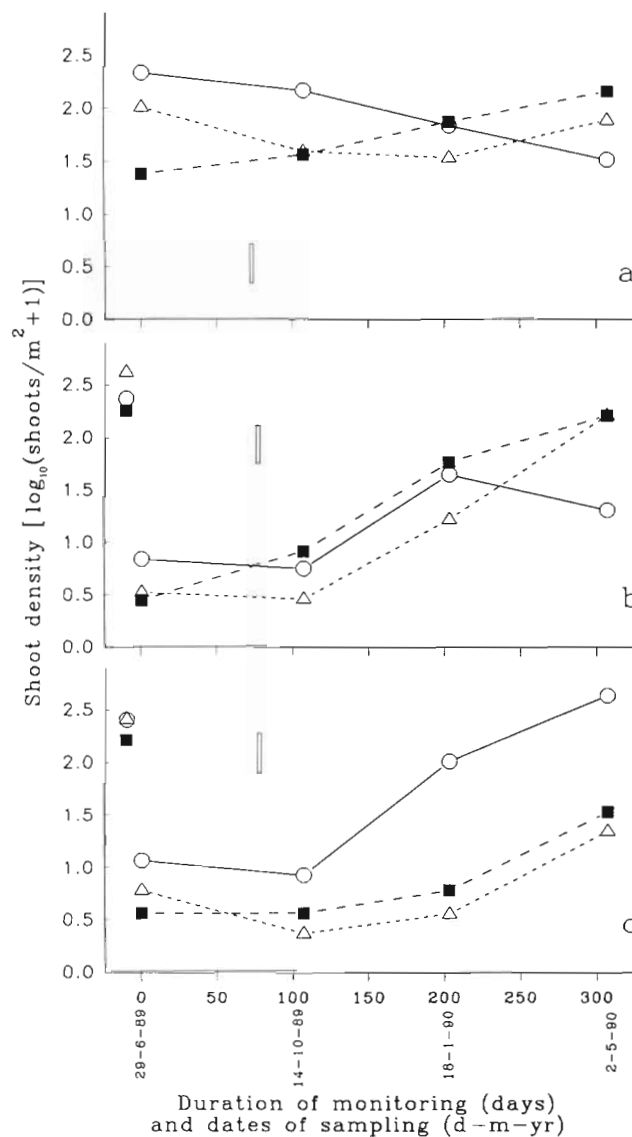


Fig. 7. Changes in shoot density of 3 species of seagrass under 3 treatments: (a) no grazing, (b) low-intensity grazing and (c) high-intensity grazing. Pretreatment shoot densities are shown on the left side of the graphs. Vertical bars: critical Least Significant Difference values for comparison between species within times. (Δ) *Halophila spinulosa*, (O) *Halophila ovalis*, (■) *Zostera capricorni*

increased over the 10 mo monitoring period, while *Halophila ovalis* decreased (Fig. 7a). *Z. capricorni* was significantly less abundant than *H. ovalis* at the start of the experiment, but significantly more abundant at the end. The abundance of *Halophila spinulosa* showed no trend. These results indicate that *Z. capricorni* was not restricted physiologically at the experimental sites. The data also suggest that *H. ovalis* may eventually be competitively excluded from this seagrass community.

Low-intensity grazing: Averaged across species and sites, 89% of shoots were removed along the simulated

Table 2. Results of analysis of variance of the exclosure experiment which examined the mean response of shoot density [$\log_{10}(\text{shoot density} + 1)$] for each experimental plot at each of 4 times involving 3 species of seagrass under 3 regimes of simulated grazing by dugongs (no grazing, low-intensity and high-intensity grazing)

Factor	Error term	df	MS	F	p
Site	Site \times Grz	2	0.598	1.84	0.2507
Grazing level (Grz)	Site \times Grz	2	5.591	17.23	0.0108
Site \times Grz		4	0.324		
Time	Time \times Site	3	3.902	7.95	0.0164
Site \times Time		6	0.491		
Species	Species \times Site	2	1.366	0.94	0.4631
Site \times Species	Site \times Species \times Grz	4	1.455		
Grz \times Time	Grz \times Time \times Site	6	1.161	26.61	0.0000
Site \times Grz \times Time		12	0.044		
Grz \times Species	Grz \times Species \times Site	4	0.951	1.14	0.4049
Site \times Grz \times Species		8	0.836		
Time \times Species	Time \times Species \times Site	6	0.413	2.23	0.1117
Site \times Time \times Species		12	0.185		
Grz \times Time \times Species	Grz \times Time \times Species \times Site	12	0.337	6.75	0.0001
Site \times Grz \times Time \times Species		24	0.050		

feeding trails (range: 78.5 to 99.2%). This reduction is in accord with the level of shoot removal from real feeding trails (72 to 99%; Preen 1993).

The seagrasses recolonised the 'feeding trails' primarily through ingrowth from the edges. The first 100 d of the experiment corresponded with winter and spring. Consequently, *Zostera capricorni*, which uniquely has a winter-spring growth period in Moreton Bay (Preen 1993), colonised the 'feeding trails' first (Fig. 7b). By the end of the experiment, *Z. capricorni* and *Halophila spinulosa* had recovered to pretreatment levels. *Halophila ovalis*, however, was significantly less abundant (Fig. 7b). These results suggest that within the seagrass community tested, disturbance from low-intensity grazing by dugongs does not alter the relative abundance of *Z. capricorni* and *H. spinulosa*, and may even reduce the relative abundance of *H. ovalis*.

High-intensity grazing: On average, 83% of seagrass shoots were removed from the plots designed to simulate intensive grazing by dugongs (range: 69.4 to 94.4%). This compares with reductions of 87, 65, 95 and 92% at grazing Areas 1, 2, 3-1 and 3-2 (Table 1).

Recovery of the seagrass within this treatment resulted from the expansion of surviving plants and possibly from seed germination. The winter-spring period at the start of the experiment retarded any recovery for the first 100 d. *Halophila ovalis* showed significantly greater recovery than *Zostera capricorni* or *Halophila spinulosa*, increasing its relative and absolute abundance particularly during the 100 to 200 d period (Fig. 7c). These data support the hypothesis that disturbance, such as that caused by the sustained grazing of a large herd of dugongs, is capable of

altering the mix of species in a seagrass meadow for a period of at least 10 mo. Fast growing species such as *H. ovalis* are apparently advantaged over high biomass species such as *Z. capricorni*.

DISCUSSION

Grazing by dugongs can constitute a major disturbance to seagrass meadows. At favoured locations, the intersecting feeding trails can cover virtually the entire substrate over large areas. At 1 site in Moreton Bay (Area 3; 41 ha) the density of seagrass shoots was reduced by 95% when it was first grazed and by 92% 6 mo later, when the partly recovered site was grazed again. On the second grazing the aboveground biomass was reduced by 96%, while 71% of the belowground biomass was removed. This impact is of a similar scale to that of some terrestrial herbivores. For example, large herds (over half a million) of wildebeest *Connochaetes taurinus albojubatus* remove 85% of green biomass as they migrate through areas (McNaughton 1976). The disturbance caused by dugong grazing differs from that of most terrestrial herbivores, however, because a substantial proportion of the belowground plant material is also consumed.

Recovery

Despite the intensity, areal extent and subsurface impact of grazing by dugong herds, the recovery of the seagrasses can be rapid (Figs. 3 & 4). This recovery is facilitated by the way dugongs feed, as well as by the growth characteristics of seagrasses. Rather than each

dugong methodically cropping all the seagrass in a series of adjoining small areas, the dugongs feed along linear, meandering feeding trails that are about as wide as their muzzles. Despite the great density of these overlapping and intersecting trails, small tufts of seagrass survive (Fig. 1c). These represent an ungrazable reserve (Noy-Meir 1975), and are the key to the resilience of the seagrass meadows in the face of intensive grazing disturbance. At Area 3, the ungrazable reserve was about 110 to 120 shoots m^{-2} (about 4% of pregrazing density). These shoots, aggregated in small tufts, sometimes linked by surviving rhizomes, act as nuclei able to expand to fill the bare gaps once grazing ceases. This regrowth is facilitated by the vegetative morphology of seagrasses, as the fragmentation of the rhizomes by feeding trails allows determinate shoots to be converted to indeterminate shoots, thus promoting proliferative growth (Tomlinson 1974).

The recovery of seagrass from grazing disturbance contrasts with recovery from disturbances caused by sedimentation, water or ice scour or some forms of die-off (Short 1983, Poiner et al. 1989). The critical difference is the effective patch size: the minimum distance between survivors capable of regeneration (Connell & Keough 1985). Hence, while an area of >50 ha may be severely disturbed by dugong grazing, the effective patch size is less than 1 m^2 , so recovery can be rapid. Areas of seagrass meadows affected by sedimentation or die off are often uniformly impacted and must recover by ingrowth from the edges, or by colonisation by seeds or other propagules. Under these circumstances recovery can take years (Birch & Birch 1984, Clarke & Kirkman 1989, Poiner et al. 1989, Preen et al. in press).

Recovery of heavily grazed seagrass meadows, however, is not invariably rapid. After the initial grazing of Area 3, no dugongs were seen at the site for 5 mo, and recovery was fast, despite the unfavourable growing season (winter). However, following the second grazing incident at this site, the recovery of the seagrass was suppressed by continued low-intensity grazing (Fig. 4), despite the favourable growing season.

Effect of grazing disturbance on species composition

The enclosure experiments showed that a disturbance, like intensive dugong grazing, can alter the relative abundance of seagrasses. Disturbance of a mixed species community encouraged *Halophila ovalis*, a pioneer species (Brouns 1987), while it retarded the expansion of *Halophila spinulosa* and *Zostera capricorni*, which is the dominant species in Moreton Bay. Such disturbance may be important in preventing *Z. capricorni* from dominating most seagrass habitats in

the study area. In Moreton Bay, *Z. capricorni* is the dugongs' least preferred species, while *H. ovalis* and *Halodule uninervis* (thin-leafed morph) are their most preferred, followed by *H. spinulosa* (assessment based on the frequency of occurrence of dugongs on seagrass communities; selective feeding within seagrass communities; and active avoidance of *Z. capricorni* patches; Preen 1993). Of all the seagrasses in Moreton Bay, *Z. capricorni* is the most fibrous, while *H. ovalis* is the least fibrous and contains the highest levels of nitrogen (Lanyon 1991).

At grazing Area 4, the changes in the relative abundance of the seagrasses reflected the pattern seen in the enclosure experiment that simulated intensive grazing. While *Zostera capricorni* was abundant at this site prior to the presumed grazing, 2 yr of data indicate that recovery to that successional stage would take at least 3 yr. In the meantime, *Halophila ovalis* dominated the site 9 to 12 mo after grazing, followed by the dominance of *Halophila spinulosa*, 18 to more than 21 mo after the grazing (Fig. 5). Thus the dugong's preferred species of seagrasses are favoured by intensive grazing, at the expense of less preferred species.

No changes in species composition were detected following disturbance by grazing at Areas 2 and 3. These sites were virtually pure stands of *Halophila ovalis* (Area 3) or *Halodule uninervis* (Area 2), both species that are adapted to disturbance (Birch & Birch 1984, Brouns 1987).

Heavy grazing pressure in terrestrial grasslands frequently converts pastures to a lower seral stage, composed of less palatable, grazing resistant species, resulting in a lower carrying capacity (Willms et al. 1988, Edroma 1989, Ralphs et al. 1990). This contrasts with the seagrasses in Moreton Bay, where heavy grazing pressure converts the meadows to a lower seral stage, dominated by a more palatable, grazing-tolerant species, probably resulting in a higher carrying capacity (see below).

Effect of grazing disturbance on forage quality

The nutritional quality of plants can increase following injury, including damage caused by herbivory (Karban & Myers 1989). The shoot nitrogen concentration of terrestrial plants (Kilcher 1981, Coppock et al. 1983) and seagrasses (Harrison & Mann 1975, Zieman et al. 1984) generally declines as the plants age and mature. However, in grasses, heavy or prolonged grazing often increases the shoot nitrogen content (Bakker et al. 1983, Coppock et al. 1983, McNaughton 1984, Jaramillo & Detling 1988, Heitschmidt et al. 1989). Seagrasses respond to cropping or clipping of leaves by increasing nitrogen levels and decreasing levels of

lignin or ash in new growth (Dawes & Lawrence 1979, Bjørndal 1980, Thayer et al. 1984, Zieman et al. 1984). Thus, concentrated grazing may allow dugongs to maximise the quality of their diet not only by increasing the area of nutritionally superior, early successional species of seagrass, but by increasing the nutritional quality of grazed seagrasses generally. This is achieved by maintaining meadows in an immature, rapidly growing state. Green turtles *Chelonia mydas* maintain seagrass patches in this growth stage (Bjørndal 1980, Ogden et al. 1980, Thayer et al. 1984, Zieman et al. 1984), as do some large terrestrial herbivores (McNaughton 1985, Edroma 1989).

Why feed in large herds?

McNaughton (1984) argues that the modification of the vegetation physiognomy is the most important impact of grazing ungulates. By reducing the grass canopy height and increasing tillage, the green biomass is concentrated closer to the ground, and the grazers increase their food-yield per bite, which can be critical to meeting the nutritional needs of large mammalian herbivores under some circumstances (Stobbs 1973, Chacon et al. 1978). Grazing by dugongs does not directly increase the food per bite, or food per dive, as the intense grazing tends to lower the biomass of seagrass. However, by disturbing large areas at a time and thus encouraging uniform recovery of favoured species, intensive, herd-based grazing achieves the equivalent of McNaughton's (1984) biomass concentration.

McNaughton (1984) further postulates that gregariousness in grazing animals may have evolved because of the increase in foraging efficiency that accrues to individuals as a result of changes in vegetation structure that follow herd grazing. He argues that while lone animals could achieve the same increase in forage-yield per bite, by concentrating their grazing in a small area, such animals would be highly subject to predation. Predation, however, has not prevented green turtles (Bjørndal 1980, Ogden et al. 1980, Thayer et al. 1984, Zieman et al. 1984) and damselfish (Sammarco 1983, Kamura & Choonhabandit 1986, Hinds & Ballantine 1987) from maintaining individual foraging patches of seagrass and algae, respectively. Solitary dugongs are prevented from farming seagrasses, not by predation, but by their mode of feeding. They feed as they swim forward, removing seagrass from long, muzzle-wide strips. For an individual dugong to efficiently disturb a substantial single area of seagrass it would have to feed along adjoining, very narrow strips. The characteristic meandering path of most feeding trails suggests that such control would be diffi-

cult to achieve. Hence, it is unlikely that individuals could change the species composition of the seagrass bed and concentrate the regrowth into distinct patches so that it could be efficiently harvested. Only by feeding in large herds, so the overlap of many meandering feeding trails results in a high intensity of disturbance over a large area, can dugongs achieve these results.

Cultivation grazing

The grazing pattern described for dugongs in Moreton Bay has profound impacts on seagrass communities. By feeding in large herds, for sustained periods, the dugongs significantly disturb large areas of seagrass. From the dugong's perspective, the subsequent changes to the seagrasses are beneficial. The nutritional quality of the regenerating seagrasses is higher than before grazing (more nitrogen, less fibre), and the improved seagrass resource is concentrated in a manner that can be harvested by the dugongs. In mixed-species communities, the abundance and concentration of nutritionally superior, early pioneer species is increased, while the expansion of the dominant, but least preferred seagrass *Zostera capricorni* into feeding areas is stalled. This grazing pattern, which may be termed cultivation grazing, is likely to be an important foraging strategy of dugongs.

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