

Impact of Dugong grazing and turtle cropping on tropical seagrass communities

LEMNUEL ARAGONES^{1,2} and HELENE MARSH^{1,3}

The impact of grazing by two megaherbivores, the Dugong *Dugong dugon* and the Green Turtle *Chelonia mydas* on the community structure of intertidal seagrasses was investigated experimentally over two time frames (shorter-term: 1–4 months; longer-term: 10 and 13 months), at three levels of grazing intensity (leaf cropping, light grazing, intensive grazing), at two seagrass meadows in tropical Queensland, Australia: (1) a mixed species bed of *Zostera capricorni*, *Halophila ovalis*, *Halodule uninervis*, *Cymodocea rotundata* and *Cymodocea serrulata*, and (2) a monospecific bed of *Halodule uninervis*. From the perspective of the megaherbivores, grazing improved the structure and dynamics of the tropical seagrass communities by altering their biomass, volume of detritus, net aboveground biomass productivity and the species composition of the mixed-species bed. Recovery from grazing disturbance occurred after several months to a year.

Key words: Seagrass, Disturbance, Grazing, Dugong, Green Turtle.

INTRODUCTION

IN the tropics and subtropics, seagrasses provide food for threatened megafauna: the Green Turtle *Chelonia mydas* (Garnett *et al.* 1985; Bjorndal *et al.* 1991; Read 1991; Brand 1995), and three species of sirenians (sea cows): the West Indian Manatee *Trichechus manatus*, the West African Manatee *Trichechus senegalensis*, and the Dugong *Dugong dugon* (Marsh *et al.* 1982, 1999; Reynolds and Odell 1991). Despite the sizes of these megaherbivores (adult Dugongs 350–400 kg; Manatees 350–1 600 kg; Green Turtles 200 kg), Thayer *et al.* (1984) assumed that their current densities are too low for them to make significant impact on seagrass communities. This assumption is unjustified in areas where densities of Dugongs and Green Turtles are high. For example, Preen (1992) estimated that about 600 Dugongs consumed 28% of the total seagrass production in favoured areas in Moreton Bay, Queensland, Australia.

Dugongs and Manatees graze destructively by uprooting seagrasses when the rhizomes are accessible (Marsh *et al.* 1982, 1999; Preen 1995; Anderson 1998). When the rhizomes are not accessible Dugongs and Manatees feed on seagrasses by cropping their leaves (Anderson 1981; Marsh *et al.* 1999), the mode of seagrass feeding used routinely by Green Turtles (Bjorndal 1980; Lanyon *et al.* 1989). These modes of foraging can have important effects on the structure of seagrass communities. Green Turtles in the Caribbean maintain “grazing plots” wherein individuals regularly recrop patches of seagrass for the younger leaf growth (Bjorndal 1980). The grazing disturbance created by Dugongs may make individual seagrass beds more desirable as Dugong habitats. In

subtropical Moreton Bay the growth of *Halophila ovalis*, a species preferred by Dugongs, is promoted while the expansion of a less favoured species, *Zostera capricorni*, is controlled (Preen 1995).

The studies conducted to investigate the effects of turtle cropping on seagrass communities have been carried out mostly in the Caribbean region (e.g., Bjorndal 1980, 1985; Ogden *et al.* 1983; Zieman *et al.* 1984). There are few similar studies for other tropical systems, particularly in Australia where Dugongs and Green Turtles are found in large numbers (Ogden 1980; Thayer *et al.* 1984; Marsh *et al.* 1995). The only studies of Dugong grazing in the tropics have been in Indonesia (de Iongh *et al.* 1995) and Thailand (Supanwanid 1996) where Dugong densities are low.

We used an experimental approach to investigate the impact of grazing by Dugongs and Green Turtles on the community structure of seagrasses at two mainland sites in the Great Barrier Reef region in tropical Australia. The study was conducted over two time frames: shorter-term (one to four months at Cardwell) and longer-term (10 months at Ellie Point and 13 months at Cardwell), and at several levels of grazing intensity: intensive grazing, light grazing, and cropping. Our experiments showed that herbivory influenced the structure and dynamics of tropical seagrass communities by altering their biomass, net aboveground biomass productivity, and the species composition of a multi-species meadow. Recovery from grazing disturbance occurred in several months to a year. We conclude that the three most important properties used in assessing the feeding niches of herbivores, the quality, quantity, and botanical

¹School of Tropical Environment Studies and Geography, James Cook University, Townsville, Australia 4811.

²Present address: Institute of Biological Sciences, University of Philippines, Los Baños College, Laguna, 4031, Philippines.

³For correspondence.

composition of vegetation (Bell 1971; Jarman 1974), are positively correlated with the intensity of grazing by Dugongs and Green Turtles in tropical seagrass ecosystems.

MATERIALS AND METHODS

Experiments were performed in the intertidal regions of the two seagrass meadows, both of which have a tidal range of approximately 3 m. The meadow at Ellie Point (16°53'S, 145°46'E) was dominated by *Zostera capricorni* (wide variety) interspersed with some *Halophila ovalis*, *Halodule uninervis*, *Cymodocea rotundata* and *C. serrulata*. The intertidal meadow at Cardwell (18°15'S, 146°01'E) consisted of *Halodule uninervis*. Some *Halophila ovalis* occurred sub-tidally in this meadow. As discussed below evidence of Dugong grazing was observed during the experiments at Cardwell, but not at Ellie Point

Longer-term experiments

Grazing simulations were carried out at each of four haphazardly chosen locations within each meadow in May-June 1993 and monitored for 11 months (Ellie Point) and 13 months (Cardwell). The four grazing treatments were arranged in a 4 × 4 Latin square at each location. The treatments of the first row and column of each Latin square were assigned randomly. PVC pipes hammered into the substrate marked the corners of the 1 m² experimental unit for each replicate. Each pipe had no more than 3 cm protruding to allow relocation while avoiding the "halo effect" that tends to occur around structures on these seagrass beds (pers. obs.). A movable quadrat fitted tightly on to these markers ensuring exact relocation of each experimental unit during the monitoring that followed the experiments. This quadrat was divided into 0.11 m² subunits using colour-coded strings enabling us to exactly relocate and re-photograph subunits within each experimental unit. Buffer zones at least 1 m wide were maintained along all sides of each experimental unit to reduce the likelihood of edge effects. We actively avoided disturbing the seagrass in these buffer zones during our fieldwork.

The four grazing treatments were as follows: (1) Intensive grazing: all aboveground material removed from experimental unit; some below ground left. This is close to the level of removal recorded in favoured Dugong feeding sites in sub-tropical Moreton Bay, where herds of Dugongs removed 96% of the aboveground biomass and 95% of the shoot density of seagrass (Preen 1992, 1995). (2) Light grazing: plants removed from three evenly-spaced 15 cm wide feeding strips within each experimental unit, all perpendicular to shore. This represented

an average removal of about 70%, 80% and 85% of the aboveground biomass of *H. ovalis*, *Zostera/Cymodocea* and *H. uninervis*, respectively. This treatment simulated the level of removal by small groups of grazing Dugongs at sites in tropical Queensland, where Dugongs have been recorded as removing an average of 63–86% of seagrass biomass from feeding trails through various species including, *H. ovalis*, *Z. capricorni*, and *H. uninervis* (Wake 1975). (3) Leaf cropping: leaves cut 1–2 cm above ground throughout each experimental unit (except for *H. ovalis* for which entire aboveground biomass removed). This treatment simulated the feeding behaviour of Green Turtles. (4) Control: undisturbed.

Shorter-term experiments

The shorter-term experiment at Cardwell was monitored for four months. This experiment was basically similar to the longer-term experiment but used four 6 × 6 Latin squares with the following treatments: (1) Light grazing harvested after four months; (2) Control for Treatment 1; (3) Cropping 1 harvested after one month; (4) Control for Treatment 3; (5) Cropping 2 harvested after two months; (6) Control for Treatment 5. Each experimental unit was reduced to 0.4356 m² to accommodate an increased number of sampling units (N = 144). Intensive grazing was not included in the treatments because the monitoring period was insufficient for recovery from this treatment.

Monitoring the grazing plots

Changes in seagrass species composition and abundance (leaf biomass only) of the subunits within each experimental unit were monitored systematically by Aragones using a vertically-held video camera (Sony video 8 Handycam, CDD-TR305E) while standing on a movable platform which fitted over the quadrat as detailed in Aragones (1996). Monitoring was performed monthly for both longer-term experiments; twice monthly for two months, then monthly for the shorter-term experiment. Evidence of natural disturbance e.g., Dugong grazing was recorded and quantified using the video camera. Grazing from fish and invertebrates was considered negligible and ignored.

The aboveground biomass (g dry weight) for each species in each frame of the video recording (which matched the relevant experimental subunit as delineated by the colour-coded strings within the movable quadrat) was estimated using a scoring scale and regression equations. The equations were calibrated by harvesting the relevant seagrasses at biomass values spanning the range encountered for each species at each site following methods outlined in the visual technique developed

for estimating the aboveground biomass and species composition of seagrasses by Mellors (1991), drying the harvest to constant weight in an oven at 60°C, and weighing it.

The essential difference between our technique and that of Mellors (1991), was that we used video images rather than direct visual estimates in the field to track changes in aboveground biomass and species composition. The video images were viewed and enhanced using a computer connected to a frame-grabber (Video Vue Image Capture, Video Associates Lab 1993). The aboveground biomass of each species in each experimental unit was calculated as the sum of the values for the corresponding subunits, estimated from the video images. The estimation of the small amounts of aboveground biomass of *Cymodocea* at Ellie Point was based on the scoring scale for *Z. capricorni* as the two could not be reliably distinguished in the video images.

The leaf biomass of seagrass removed from each experimental unit at Cardwell by natural Dugong grazing was estimated visually from the video images. The feeding scars were very distinct and could be monitored through time by simultaneous viewing of a temporal series of images. The estimates of aboveground biomass for each experimental unit were adjusted to compensate for any seagrass removed naturally by Dugongs.

Seagrass samples from the experimental units were harvested at the end of the monitoring period at each site. They were washed, sorted, dried and weighed in order to measure total biomass, and aboveground and belowground biomass. These weights were used to assess the accuracy of the corresponding visual estimates of aboveground biomass empirically. Detritus (species pooled) was separated from the samples harvested from Ellie Point only during sorting, and dried and weighed as above.

An exact measurement of net primary productivity could not be obtained because we did not attempt the following measurement: below-ground biomass production, biomass due to excretion, death and decomposition, and harvest by smaller herbivores such as fish. An index of the net aboveground biomass production (INABP g dw/m²) was determined by summing the aboveground biomass accumulated per month over the duration of the experiment using the following equation:

where χ_{ai} is either: (1) aboveground biomass for species *a* at time *i*, or (2) aboveground biomass for all species combined at time *i* (starting from the first month of recovery) and *n* is the number of months of the experiment.

Statistical analyses

The effects and interactions relevant to the experimental treatments are discussed in this paper. The full ANOVA tables are in Aragonés (1996). The main effects and interactions are discussed only if the higher order interactions were not significant.

Temporal response of the aboveground biomass to the treatments

The response (g dw/m²) of the aboveground biomass of seagrass to the various treatments was examined using repeated measures univariate ANOVAs (the corresponding multivariate tests had low power). Separate repeated measures ANOVAs were performed for each species, because the results of the repeated measures ANOVA considering all species simultaneously were complex and difficult to interpret (Aragones 1996). The values for the various experimental units for each treatment within each Latin square were aggregated to account for location being a random factor. The probabilities of Epsilon corrected *F* values (Greenhouse-Geisser Epsilon) were calculated to compensate for deviations from univariate assumptions.

Effects of the grazing treatments on seagrasses at harvest

Factorial ANOVAs were used to test the effects of grazing treatment, species (Ellie Point only), location and their interactions on the biomass of the harvested plant parts at the end of each experiment. In the shorter-term experiments, similar analyses were performed using the paired treatment-controls as outlined above and in Table 2.

RESULTS

The effects of grazing and cropping: longer-term experiments in the mixed-species seagrass bed at Ellie Point

There were differences in the species composition and leaf biomass among the four experimental locations in this seagrass bed prior to our manipulation. The leaf biomass of *H. ovalis* (13.9 s.e. 0.86 gdw/m²) was almost equal to that of *Zostera/Cymodocea* (12.3 s.e. 0.54 gdw/m²) at Location A, where smaller amounts of *H. uninervis* (3.2 s.e. 1.21 gdw/m²) also occurred. Location B was dominated by *H. ovalis* (15.1 s.e. 1.75 gdw/m²) interspersed with some *Zostera/Cymodocea* (6.3 s.e. 1.63 gdw/m²) with traces of *H. uninervis* (0.13 s.e. 0.05 gdw/m²). *Zostera/Cymodocea* dominated Locations C (19.3 s.e. 0.61 gdw/m²) and D (20.5 s.e. 1.33 gdw/m²) with very sparse *H. ovalis* (6.2 s.e. 0.20 gdw/m² at Location C; 0.5 s.e. 0.38 gdw/m² at Location D) and no *H. uninervis*.

Temporal changes in the seagrasses in the control plots

The combined leaf biomass of all species reached a low in June and increased in March after the wet season (Fig. 1a). The leaf biomass of *H. ovalis* declined to a low in November and increased from December until the March harvest (Fig. 1b). The leaf biomass of *Zostera/Cymodocea* was low between June and August (winter), lowest in February, and increased in March (Fig. 1c). The leaf biomass of *Halodule uninervis* was very low and almost constant throughout the experiment (Fig. 1d).

Repeated measures analysis of variance

The grazing treatment by time interaction was highly significant for both *H. ovalis* and *Zostera/Cymodocea* but not for *Halodule uninervis* (Table 1). The effect of intensive grazing over the experiment varied by species: the leaf biomass of *H. ovalis* increased (Fig. 1b) as that of *Zostera/Cymodocea* decreased (Fig. 1c). Our failure to detect change in *H. uninervis* may have been confounded by the low biomass and high spatial variability of this species at Ellie Point (Fig. 1d). The effects of the grazing treatments were locally variable for each species as evidenced by the highly significant location \times time interactions (Table 1).

Recovery

The recovery of the seagrass community at Ellie Point from the different regimes of simulated herbivory was relatively rapid (Fig. 1a). Even the intensive grazing plots recovered within seven months. Recovery from light grazing and cropping occurred within three months.

Halophila ovalis: The plots exposed to cropping and light grazing recovered within two months (Fig. 1b); those exposed to intensive grazing had the slowest (three months) recovery but the greatest in terms of changes to the above-ground biomass. After 10 months, the leaf biomass of *H. ovalis* subjected to light and intensive grazing was significantly higher than the controls (Fig. 1b). The cropping treatment was similar to the control at this time (Fig. 1b).

Zostera/Cymodocea: These species did not recover from the grazing treatments quite as rapidly as *H. ovalis* (Fig. 1c). Recovery from cropping took two months; from light

grazing, three months, from intensive grazing eight months.

Effect of intensity of herbivory on community composition

The species composition of the seagrass plots exposed to both intensive and light grazing switched in dominance from *Zostera/Cymodocea* to *H. ovalis* (Figs 1b,c). In the intensive grazing treatment, the leaf biomass of *H. ovalis* was half that of *Zostera/Cymodocea* at the beginning of the experiment in May 1993. By the following March, the leaf biomass of *H. ovalis* was twice that of *Zostera/Cymodocea*.

Biomass on harvesting

After 10 months, the grazing treatment by species interaction was significant only for the leaf fraction (Table 1), that is, the leaf biomass of intensely grazed *H. ovalis* was significantly higher than that of the control (Fig. 1e); the biomass of the other species was similar to the control. The ratio of leaf to roots/rhizome biomass was significantly affected by the treatments (Table 1 and Fig. 1f); the ratio of the roots/rhizomes to the leaves at the intensive grazing plots was significantly lower than that of the controls. The ratio also varied by species. *Zostera/Cymodocea* had a higher ratio of roots/rhizomes to leaves than *H. ovalis* (Fig. 1f) for all treatments including the controls. Treatment did not have a significant effect on the biomass of either the roots/rhizomes or the whole plants (Table 1).

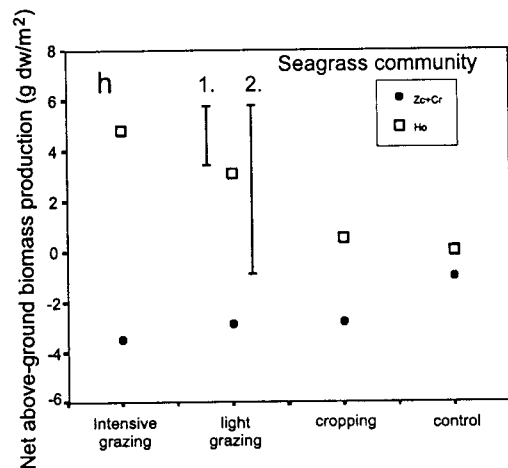
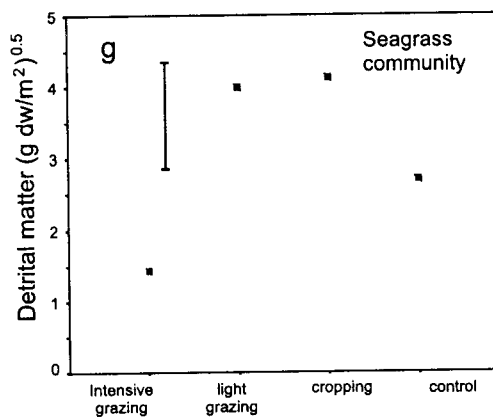
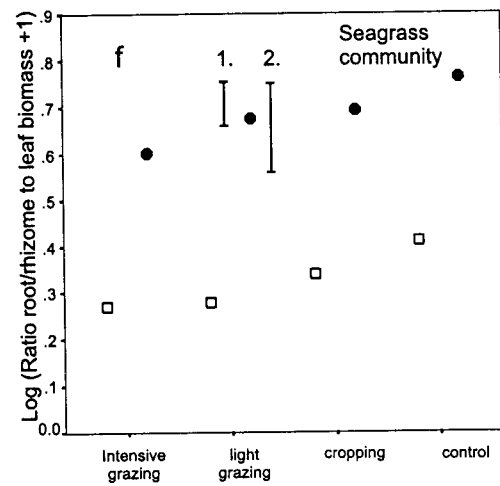
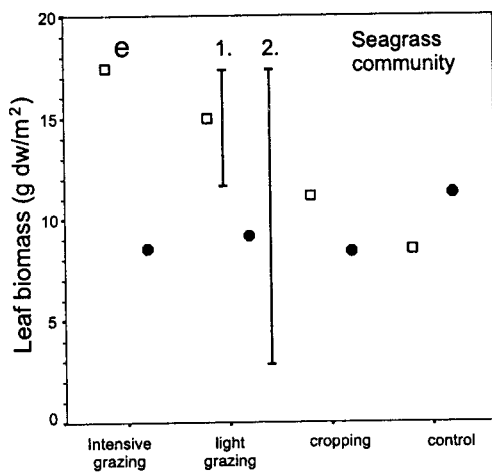
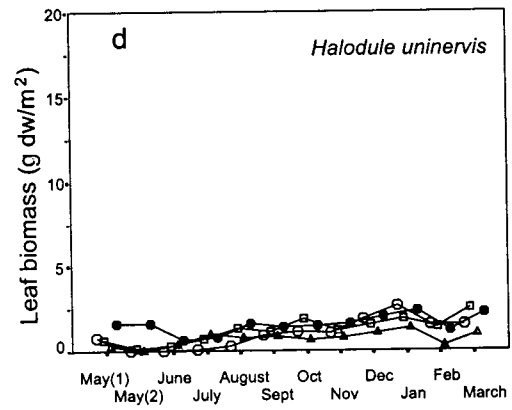
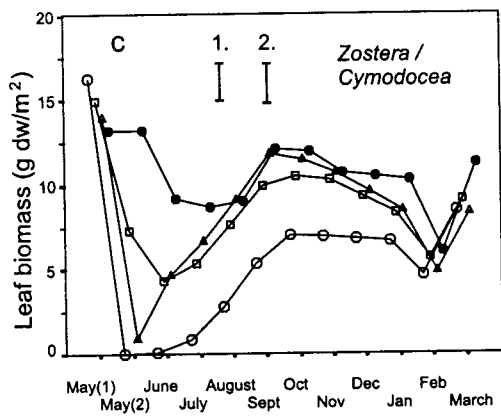
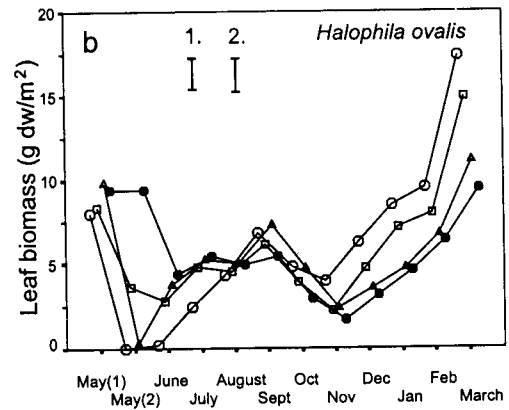
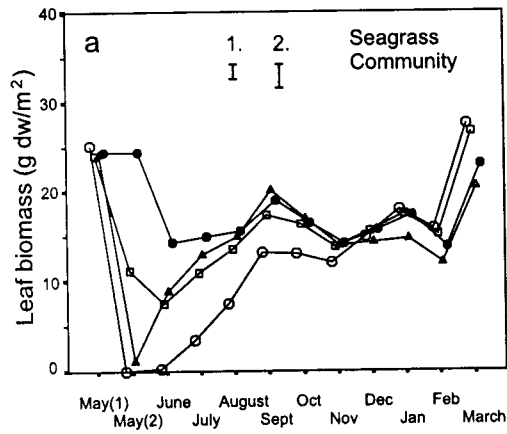
Detritus on harvesting

Most of the detritus resulted from *Zostera/Cymodocea* shedding leaf sheaths. Ten months after the grazing treatments, the intensive grazing plot had significantly less leaf detritus than the controls (Fig. 1g and Table 1). The detritus in the light grazing and cropping plots did not differ from those of the controls (Fig. 1g).

Index of net aboveground biomass production

Herbivory affected the index of net above-ground biomass production (INABP) variably, depending on the species of seagrass (Fig. 1h). The INABP of *H. ovalis* was significantly higher than the controls and increased with the intensity of herbivory. In contrast, the

Fig. 1 (opposite). The response of the multi-species seagrass meadow at Ellie Point to treatments in the longer-term grazing experiment; (a-d) temporal response (g dw/m²) monitored using video of the aboveground biomass of: (a) seagrass community, (b) *Halophila ovalis* (Ho), (c) *Zostera/Cymodocea* (Zc+Cr), (d) *Halodule uninervis* (Hu); (e-h) response (g dw/m²) at harvest after 10 months for (e) leaf biomass, (f) ratio of root/rhizome to leaf biomass, (g) detrital matter, (h) net aboveground biomass production. Bars represent the Least Significant Difference (LSD) between means showing differences among: (a-c) 1. treatments within time and 2. times within treatment; (e-f, h) 1. treatments within species and 2. species within treatment, (g) treatments. May (1) = before and (2) = after, simulation measurements were carried out.



INABP of *Z. capricorni* decreased as the level of herbivory increased.

The effects of grazing and cropping: longer-term experiments in the monospecific seagrass bed at Cardwell

Leaf biomass removed by Dugongs

Dugongs grazed within the study area from August (1993) through June (1994), inclusive

(Fig. 2b). Based on the estimated leaf biomass removed, the major grazing events occurred during November-December (1993), February-March, March-April and May-June.

Control plots

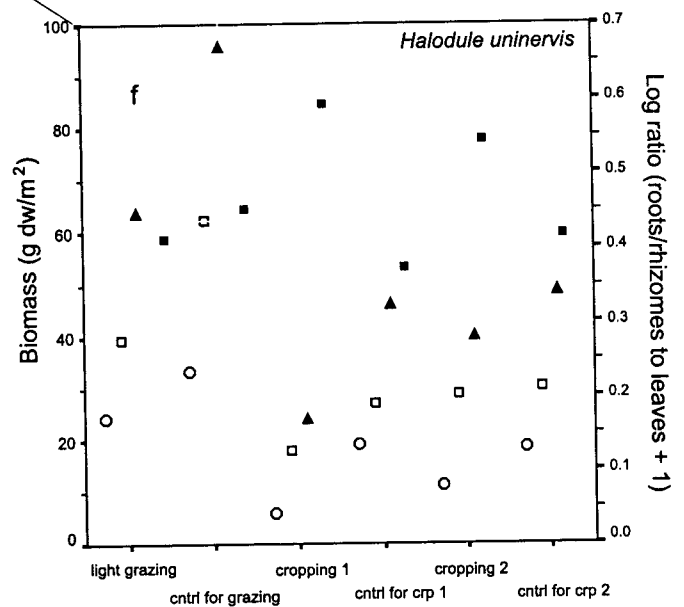
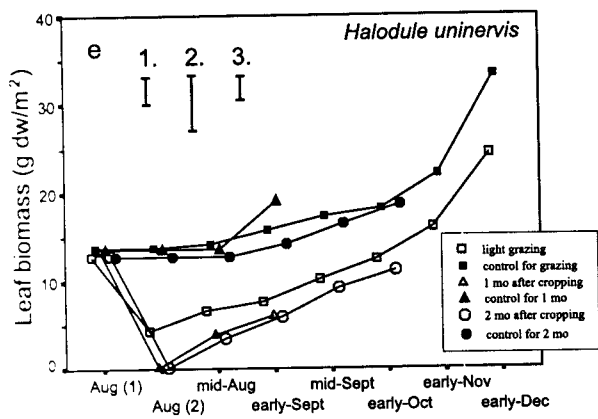
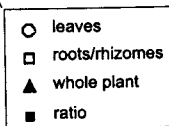
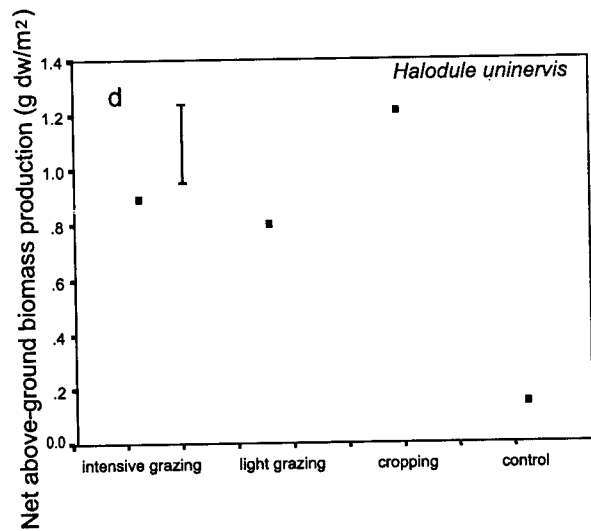
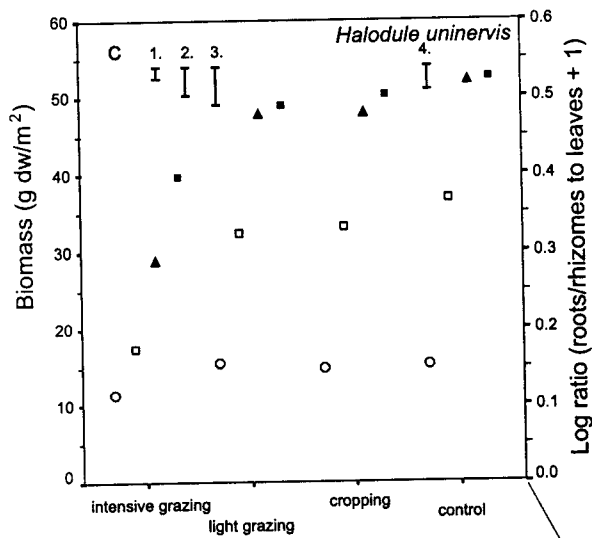
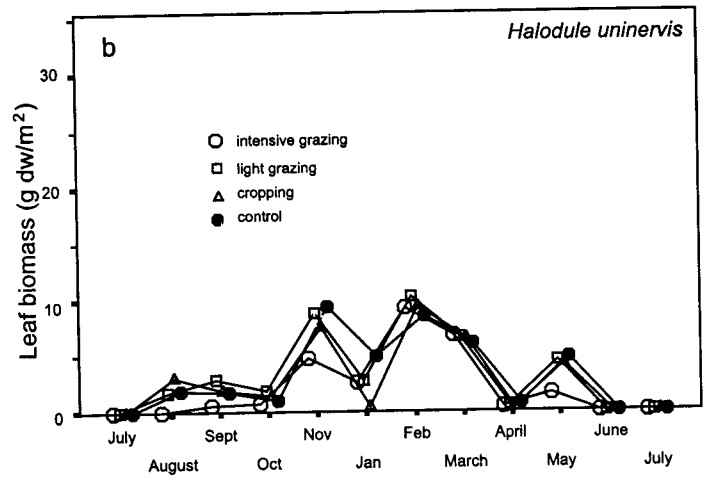
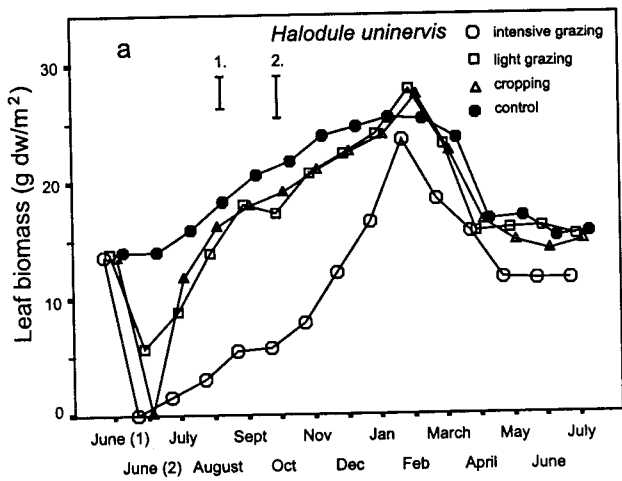
The aboveground biomass of *Halodule uninervis* in the control plots changed uni-modally over time (Fig. 2a). It was lowest at the start of the experiment in June, gradually increased to

Table 1. Results for the salient terms in the ANOVAs for the longer-term (10 and 13 months) grazing experiments at Ellie Point and Cardwell. Significant p values are in bold.

Response	Df	Df error	MS	F	P (GG) ¹	Df	Df error	MS	F	P (GG) ¹
Ellie Point: a multispecies seagrass meadow										
<i>Repeated measures of aboveground biomass using video</i>										
	Grazing Treatment × Time Interaction ^{2,3}					Location × Time Interaction ^{2,3}				
<i>H. ovalis</i>	30	90	19.84	7.07	<0.001 (0.001)	30	90	19.54	6.97	<0.001 (0.001)
<i>H. uninervis</i>	30	90	0.67	1.02	0.455 (0.45)	30	90	4.41	6.68	<0.001 (0.001)
<i>Zostera/Cymodocea</i>	30	90	18.76	5.29	<0.001 (0.003)	30	90	30.82	8.69	<0.001 (0.001)
<i>Biomass on harvesting: H. ovalis and Zostera/capricorni only</i>										
	Species × Grazing Treatment ^{2,4}					Grazing Treatment ^{2,5}				
Leaves	3	9	199.70	4.04	0.045	3	9	82.15	7.67	0.008
Roots/rhizomes	3	9	1 362.75	2.08	0.174	3	9	596.71	1.66	0.246
Whole plants	3	9	2 604.62	2.57	0.119	3	9	280.30	0.68	0.589
Ratio roots+rhizomes/leaves ⁶	3	9	0.01	0.21	0.889	3	9	0.13	6.41	0.013
INABP	3	9	85.98	10.54	0.003	3	9	14.56	4.64	0.032
Detritus						3	9	25.46	7.30	0.009
Cardwell: a monospecific seagrass meadow										
<i>Repeated measures of aboveground biomass using video</i>										
	Grazing Treatment × Time Interaction ^{2,3}					Location × Time Interaction ^{2,3}				
<i>H. uninervis</i>	39	117	36.39	15.26	<0.001 (0.001)	39	117	11.74	4.92	<0.001 (0.001)
<i>Biomass on harvesting: H. uninervis</i>										
	Grazing Treatment ^{2,5}									
Leaves	3	9	57.15	16.14	0.001					
Roots/rhizomes	3	9	1 198.39	56.61	<0.001					
Whole plants	3	9	1 762.95	48.57	<0.001					
Ratio roots+rhizomes/leaves ⁶	3	9	0.05	48.18	<0.001					
INABP	3	9	3.47	32.09	<0.001					

¹ With Greenhouse-Gieser correction for correlation through time in repeated measures; ² All factors fixed except location, which was random; ³ Tested against within subjects residual; ⁴ Tested against location × species × treatment; ⁵ Tested against location × treatment; ⁶ Transformed log (ratio+1).

Fig. 2 (opposite). The response of the monospecific seagrass meadow at Cardwell to treatments in the longer- and shorter-term grazing experiments. (a) temporal response (g dw/m²) monitored using video of the aboveground biomass of *Halodule uninervis* during the longer-term experiment; (b) leaf biomass (g dw/m²) removed naturally by Dugong over time during the longer-term experiment (note: December is not shown in this figure because there was no monitoring for this month due to inaccessibility of experimental units); (c-d) response (g dw/m²) at harvest after 13 months for (c) seagrass plant parts, (d) net aboveground biomass production; (e) temporal response (g dw/m²) monitored using video of the aboveground biomass of *Halodule uninervis* during the shorter-term experiments (1-4 months); (f) response (g dw/m²) at harvest after 1-4 months exposure to treatments in the short-term experiments. Bars represent the Least Significant Difference (LSD) between means showing differences among: (a) 1. treatments within time and 2. time within treatments; (c) treatments for 1. leaves, 2. roots/rhizomes, 3. whole plant, 4. ratio (corresponds with right axis); (d) treatments; (e) time within treatments of: 1. light grazing/control, 2. 1 month after cropping/control, 3. 2 months after cropping/control. The LSDs are not necessary for (f) as comparisons are summarised in Table 2. June and August (1) = before and (2) = after simulation measurements were carried out.



peak in January-February and declined again from March to July. This trend was similar across all treatments (Fig. 2a).

Recovery

The aboveground biomasses of the plots exposed to the light grazing and cropping treatments were similar to the control plots after the third month (Fig. 2a). The biomass of the intensive grazing plots recovered to a level similar to the controls after eight months, coincident with the peak of the aboveground biomass (February), then declined again, and was significantly lower than the remaining treatments after 11 months (Fig. 2a). Recovery may have been prolonged by the occurrence of repeated natural Dugong grazing within the experimental units (Fig. 2b).

Biomass upon harvesting

After 13 months, the biomass of the leaf, root/rhizome fractions, whole plants and the ratio of leaf to roots/rhizomes of *H. uninervis* were still significantly affected by the treatments (Table 1). Values for the intensive grazing treatment were significantly less than those of the control plots (Fig. 2c).

Grazing and the index of net aboveground biomass production

The intensity or level of herbivory significantly affected the index of net aboveground biomass production (INABP) of *H. uninervis* (Fig. 2d, Table 1). The INABP was significantly higher in the treatments than the controls, with the cropping treatment exhibiting the highest levels followed by intensive grazing and light grazing (Fig. 2d).

The effects of grazing and cropping: shorter-term experiments in the monospecific seagrass bed at Cardwell

The leaf biomass of the various controls was always greater than that of any of the other treatments as all the experiments were concluded before complete recovery (Fig. 2e). Except for the ratio of the roots/rhizomes to leaves, the responses to the cropping treatment harvested after one month tended to be variable across locations (Table 2). The ratio of the biomass of the roots/rhizomes to that of the leaves was significantly less than the controls (Fig. 2f). After two months the effect of the cropping treatment was significant only for the leaves; the leaf biomass was considerably

Table 2. Results for the salient terms in the ANOVAs for the shorter-term (1–4 months) grazing experiment in the monospecific meadow at Cardwell. Significant p values are in bold.

Response	Df	Df error	MS	F	P (GG) ¹	Df	Df error	MS	F	P (GG) ¹
Cardwell: a monospecific seagrass meadow										
<i>Repeated measures of aboveground biomass of H. uninervis using video</i>										
		Grazing Treatment × Time Interaction ^{2,3}					Location × Time Interaction ^{2,3}			
Light grazing (T1) and control (T2): 4 months	7	21	10.48	14.18	<0.001 (0.002)	21	21	1.16	1.56	0.157 (0.28)
Cropping (T3) and control (T4): 1 month	3	9	56.3	23.36	<0.001 (0.011)	9	9	1.67	0.69	0.702 (0.63)
Cropping (T5) and control (T6): 2 months	5	15	26.13	50.61	<0.001 (<0.001)	15	15	0.60	1.16	0.387 (0.44)
<i>Biomass on harvesting: H. uninervis</i>										
		Light grazing: 4 months ^{2,4,5}					Cropping: 1 month ^{2,6}			
		Treatment					Location × Treatment Interaction			
Leaves	1	3	964.67	26.86	0.014	3	40	144.18	29.44	<0.001
Roots/rhizomes	1	3	6 314.4	38.12	0.009	3	40	231.15	5.77	0.002
Whole plants	1	3	1 222.15	36.97	0.009	3	40	733.52	11.76	<0.001
Ratio roots+rhizomes/leaves ⁷	1	3	0.02	25.06	0.015	3	40	0.01	1.84	0.156
INABP	1	3	0.47	3.23	0.170	3	40	8.29	8.23	0.000
		Cropping: 2 months					Cropping: 2 months			
		Location × Grazing Treatment Interaction ^{2,6}					Grazing Treatment ^{2,4}			
Leaves	3	40	27.51	1.64	0.196	1	3	669.43	24.34	0.016
Roots/rhizomes	3	40	128.69	1.42	0.251	1	3	20.17	0.16	0.719
Whole plants	3	40	127.47	0.77	0.519	1	3	921.99	7.23	0.074
Ratio roots+rhizomes/leaves ⁷	3	40	0.02	5.90	0.002	1	3	0.19	7.84	0.068
INABP	3	40	0.11	0.19	0.903	1	3	14.91	132.99	0.001

¹ With Greenhouse-Gieser correction for correlation through time in repeated measures; ² All factors fixed except location, which was random; ³ Tested against within subjects residual; ⁴ Tested against within location × treatment; ⁵ Location × treatment interactions not significant; ⁶ Tested against within location × species × treatment; ⁷ Transformed log (ratio + 1).

less than the corresponding undisturbed plots (Table 2, Fig. 2f). The effect of the grazing treatment on the ratio of roots/rhizomes to leaves was variable across locations within the meadow (Table 2). After four months, the effect of the light grazing treatment was still significant as evidenced by the biomass of both plant parts and whole plants still being lower than their controls, and a smaller ratio of roots/rhizomes to leaves (Table 2, Fig. 2f).

DISCUSSION

Our experiments demonstrated that the simulated levels of grazing by large marine herbivores influenced both the community structure and dynamics of tropical seagrasses. The nature and extent of the effects were related to: (1) the intensity (and timing) of the grazing impact and its location within the meadow; and (2) the nature of the seagrass community, including its species composition which may be confounded with location within the meadow. Recovery times varied from months for *H. ovalis* and *Zostera/Cymodocea* at Ellie Point to more than one year for *H. uninervis* at Cardwell.

Species composition

At Ellie Point, a meadow dominated by *Zostera/Cymodocea*, both light and intensive grazing changed the species composition of the community in favour of *H. ovalis* at the expense of *Zostera/Cymodocea* (Fig. 1b,c). This contrasts with Preen's (1992) findings from experiments which were conducted at the same time of year in subtropical Moreton Bay which showed a significant increase in *H. ovalis* at the expense of *Z. capricorni* as a result of intensive grazing only. This discrepancy can be explained by regional differences in growth. In Moreton Bay, *Z. capricorni* has a winter-spring growth period, while at Ellie Point, it has a spring growth period (McKenzie 1994; and this study) Thus, the timing of grazing disturbance may influence the course of recovery differentially at different locations.

We observed no changes in the species composition of the monospecific bed of *H. uninervis* at Cardwell after the grazing treatments, despite the presence of *H. ovalis* subtidally. Preen (1992) also reported no post-grazing changes in species composition in monospecific stands of *H. ovalis* and *H. uninervis* in Moreton Bay. Preen argued that these species are adapted to disturbance because of their opportunistic life history strategies. The growth rate of *H. ovalis* is faster and the turnover time shorter than *Z. capricorni* and *C. rotundata* (Table 3), clearly demonstrating why *H. ovalis* is more able to respond to disturbance than these other species. We were not able to find any

corresponding data for *H. uninervis*, but it is considered to be an opportunistic species like *H. ovalis* (e.g., see Den Hartog 1970; Lanyon 1991; Preen 1992; Lee Long *et al.* 1993) and is likely to have high specific growth rates and turnover times.

Table 3. Relative growth rates, from the published literature, of some Australian tropical seagrasses.

Species	Specific growth rate (% per day)	Turnover time (days)	
<i>H. ovalis</i>	4.0–9.0	11–24	Hillman and McComb (1988)
<i>Z. capricorni</i>	0.8–3.5	33–67	Kirkman <i>et al.</i> (1982); Larkum <i>et al.</i> (1984, 1989)
<i>C. rotundata</i>	2.5–4.0	25–40	Brouns (1987)

Detritus

Grazing also altered the relative abundance of detritus matter at Ellie Point. The intensive grazing plots had considerably less detritus matter than the other treatments (Fig. 1g), presumably because most of the plant material was from new growth.

Aboveground biomass

H. ovalis is a favoured food of Dugongs and juvenile Green Turtles in Moreton Bay (Preen 1992 for Dugongs; Read 1991, Brand 1995 for Green Turtles). In the tropics, Dugong feeding trails have often been reported from stands dominated by *H. ovalis* (e.g., Wake 1975; Anderson and Birtles 1978, tropical Queensland; Aragones 1994, Philippines; Supanwanid 1996, Thailand), indicating that this species must be an important food item. This conclusion is supported by the analysis of the stomach contents of Dugongs from Queensland (Marsh *et al.* 1982). The leaves of *H. ovalis* are the most digestible of the seagrasses studied by Aragones (1996), and in general, the leaves have higher concentrations of nitrogen than the root/rhizome fraction (Lanyon 1991; Aragones 1996). After 10 months, the aboveground biomass of *H. ovalis* was similar to the below-ground biomass in grazed plots indicating that grazing induces the growth of leaves relative to rhizomes. This should be advantageous both to Dugongs and Green Turtles as the leaves have higher concentrations of nitrogen than the roots and rhizomes (Aragones 1996).

According to the grazing optimization hypothesis developed for terrestrial grazers, aboveground net primary productivity is maximized at some optimal grazing level (McNaughton 1979; Hilbert *et al.* 1981; Dyer *et al.* 1982). Plants growing at a rate close to their maximum potential relative growth rate

have less opportunity to respond positively to grazing than plants with realized growth rates far below maximum. As grazing intensity increased at Ellie Point, we observed an increase in our index of net aboveground biomass productivity (INABP) for *H. ovalis*. In contrast, the INABP for *Zostera/Cymodocea* decreased (Fig. 1h). This result suggests that *H. ovalis* has a greater capacity to compensate for Dugong grazing than the other species studied and may be a species tolerant of herbivory.

Recovery

Recovery of the seagrasses from grazing disturbance depended on the timing and intensity of the grazing disturbance, the species composition and location within the beds (which may be confounded), and the occurrence of additional disturbance. In our experiment at Ellie Point (Fig. 1b-d), *H. ovalis* recovered most quickly, followed by *H. uninervis*, then lastly *Z. capricorni*. As detailed above, *H. ovalis* has faster specific growth rate and turnover time than *Z. capricorni* and probably *H. uninervis*.

At Ellie Point, both *H. ovalis* and *Zostera/Cymodocea* recovered rapidly from intensive and light grazing, despite the treatments being applied in the dry season, when growth is lowest. In Thailand, recovery of *H. ovalis* from Dugong grazing was also rapid (two months) during the dry season (Supanwanid 1996), when its growth is supposedly at its lowest. Despite similar timing of the grazing experiments, *Z. capricorni* recovered more rapidly from light grazing (within five months) at Ellie Point in the tropics than in Moreton Bay in the sub-tropics (6.5–10 months).

The recovery of *H. uninervis* at Cardwell took longer (eight months) than in simulations in Indonesia and Moreton Bay. However, we conducted our experiments in winter (dry season), whereas de Jongh *et al.* (1995) conducted their research at a lower latitude in Indonesia over the wet season. Preen (1992) performed his experiments in Moreton Bay during the summer and autumn growing seasons. In general, the effect of the timing of grazing disturbance on the recovery period of seagrasses in sub-tropical Moreton Bay was more pronounced than suggested by the studies in the tropics, presumably because of the more pronounced seasonality in the sub-tropics.

A confounding factor in our experiments conducted at the monospecific seagrass bed in Cardwell was the repeated grazing that occurred within the experimental plots (Fig. 2b). Grazing by Dugongs may have contributed to the decline in leaf biomass in the first half of 1994 (Fig. 2a). However, the influence

of environmental factors such as the variation in daytime tidal exposure and the seasonal pattern of growth of *H. uninervis* cannot be eliminated.

In Moreton Bay, Preen (1995) suggested that the recovery of *H. uninervis* beds from Dugong grazing can be suppressed, especially after low levels of sustained grazing pressure follow recovery. Overall, the recovery of seagrasses from grazing varies according to species, location and timing of the disturbance. As our experiments were conducted during the autumn-winter season, which is the period of slow growth, we predict that tropical seagrasses will recover even more rapidly from grazing disturbance which occurs at other times of the year.

Scale of disturbance

The scale of disturbance from grazing differs from that of non-grazing disturbances. Natural disturbances such as sedimentation water scouring, or "die-off" from disease, flooding or cyclones may cause a uniform loss of tropical seagrasses over large areas. Meadows suffering such losses take years to recover (Short 1983; Poiner *et al.* 1989; Preen 1992; Poiner and Peterken 1995; Preen *et al.* 1995). In contrast, grazing disturbance is limited by the feeding behaviour of the grazer. For example, Dugongs generally feed by uprooting whole plants from linear, serpentine feeding trails that are about as wide as their muzzle (Heinsohn *et al.* 1977; Anderson and Birtles 1978; Preen 1992). Preen (1995) observed that the presence of seagrass patches of less than 1 m², interspersed across quite large areas (>50 ha) which have been severely disturbed by Dugongs. These patches of seagrasses survive even the most intensive regime of grazing, forming a reserve which is not accessible to Dugongs. Preen (1992) suggests that this "ungrazable reserve" is the key to seagrasses recovering within months from intensive Dugong grazing.

ACKNOWLEDGEMENTS

Thanks are due to the following organisations and individuals: AUSAID for Aragon's Ph.D. scholarship, the Great Barrier Reef Marine Park Authority and James Cook University for research funds, the Cairns Port Authority for access to Ellie Point, Tony Preen, Jane Mellors and the Seagrass Ecology Group of the Queensland Department of Primary Industries for technical advice, Glen De'ath and especially Steve Delean for statistical support, Carole Eros for assistance with manuscript preparation and numerous volunteers who survived the mud and sandflies characteristic of tropical intertidal seagrass meadows in north Queensland.

REFERENCES

- Anderson, P. K., 1981. Dugong behaviour: observations, extrapolations, and speculations. Pp. 54-64 in *The Dugong*. Proc. Seminar/workshop 8-13 May 1979 ed by H. Marsh. Dept. Zoology, James Cook University.
- Anderson, P. K., 1998. Shark Bay Dugongs (*Dugong dugon*) in summer. II: Foragers in a Halodule-dominated community. *Mammalia* **62**: 409-25.
- Anderson, P. K. and Birtles, A., 1978. Behaviour and ecology of the Dugong, *Dugong dugon* (Sirenia): Observations in Shoalwater and Cleveland bays, Queensland. *Aust. Wildl. Res.* **5**: 1-23.
- Aragones, L., 1994. Observations on Dugongs at Calauit Island, Busuanga, Palawan, Philippines. *Wild. Res.* **21**: 709-17.
- Aragones, L., 1996. Dugongs and Green Turtles: Grazers in the Tropical Seagrass Ecosystem. Ph.D. thesis, James Cook University.
- Bell, R. H. V., 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* **225**: 86-93.
- Bjorndal, K. A., 1980. Nutrition and grazing behaviour of the Green Turtle *Chelonia mydas*. *Mar. Biol.* **56**: 147-54.
- Bjorndal, K. A., 1985. Nutritional ecology of sea turtles. *Copeia* **3**: 736-51.
- Bjorndal, K. A., Suganuma, H. and Bolten A. B., 1991. Digestive fermentation in Green Turtles *Chelonia mydas*, feeding on algae. *Bull. Mar. Sci.* **48**: 166-71.
- Brand, S. J., 1995. Diet Selection by Juvenile Green Turtles *Chelonia mydas*, in Subtropical Flathead Gutter, Moreton Bay. Honours thesis. University of Queensland.
- Brouns, J. J. W. M., 1987. Aspects of production and biomass of four seagrass species (Cymodoceidae) from Papua New Guinea. *Aquat. Bot.* **27**: 333-62.
- De Iongh, H. H., Wenno, B. and Meelis, E., 1995. Seagrass distribution and seasonal biomass changes in relation to Dugong grazing in the Moluccas, East Indonesia. *Aquat. Bot.* **50**: 1-19.
- Den Hartog, C., 1970. *Seagrasses of the World*. North-Holland Publishing Co., Amsterdam.
- Dyer, M. I., Detling, J. K., Coleman, D. C. and Hilbert, D. W., 1982. The Role of Herbivores in Grasslands. Pp. 255-95 in *Grasses and Grasslands* ed by J. R. Estes, R. J. Tylr and J. N. Brunken. University of Oklahoma Press, Norman, Oklahoma.
- Garnett, S. T., Price, I. R. and Scott, F. J., 1985. The diet of the Green Turtle, *Chelonia mydas* in Torres Strait. *Aust. Wildl. Res.* **12**: 103-12.
- Heinsohn, G., Wake, J., Marsh, H. and Spain, A., 1977. The Dugong (*Dugong dugon* (Muller)) in the seagrass system. *Aquaculture* **12**: 235-48.
- Hilbert, D. W., Swift, D. M., Detling, J. K. and Dyer, M. I., 1981. Relative growth rates and grazing optimization hypothesis. *Oecologia* **51**: 14-18.
- Hillman, K. and McComb, A. J., 1988. The primary production of the seagrass *Halophila ovalis* in the Swan/Canning estuary, western Australia. II. Seasonal changes in productivity and morphology. Pp. 635-85 in *Biology of Seagrasses* ed by A. Larkum, A. McComb and S. Shepherd. Elsevier, New York.
- Jarman, P. J., 1974. The social organisation of antelope in relation to their ecology. *Behaviour* **48**: 215-67.
- Kirkman, H., Cook, I. H. and Reid, D. D., 1982. Biomass and growth of *Zostera capricorni* Aschers in Port Hacking, N.S.W. Australia. *Aquat. Bot.* **12**: 57-67.
- Lanyon, J., 1991. The Nutritional Ecology of the Dugong *Dugong dugon* in Tropical North Queensland. Unpublished Ph.D. thesis, Monash University, Clayton, Victoria, V. I and II.
- Lanyon, J., Limpus, C. and Marsh, H., 1989. Dugongs and Turtles: Grazers in the Seagrass System. Pp. 610-34 in *Biology of Seagrasses* ed by A. Larkum, A. McComb and S. Shepherd. Elsevier, New York.
- Larkum, A. W. D., Collett, L. C. and Williams, R. J., 1984. The standing crop, growth and shoot production of *Zostera capricorni* Aschers in Botany Bay, New South Wales, Australia. *Aquat. Bot.* **19**: 307-27.
- Larkum, A. W. D., McComb, A. J. and Shepherd, S. A. (eds), 1989. *Biology of Seagrasses*. A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.
- Lee Long, W., Mellors, J. E. and Coles, R. G., 1993. Seagrasses between Cape York and Hervey Bay, Queensland, Australia. *Aust. J. Mar. Freshwater Res.* **44**: 33-42.
- Marsh, H., Channells, P., Heinsohn, G. and Morrissey, J., 1982. Analysis of stomach contents of Dugongs from Queensland. *Aust. Wildl. Res.* **9**: 55-67.
- Marsh, H., Corkeron, P. J., Limpus, C. J., Shaughnessy, P. D. and Wards, T. M., 1995. The reptiles and mammals in Australian seas: their status and management. Pp. 151-66 in *State of the Marine Environment Report for Australia*, Technical Annex: 1 Great Barrier Reef Marine Park Authority, Townsville.
- Marsh, H., Beck, C. A. and Vargo, T., 1999. Comparison of the capabilities of Dugongs and West Indian Manatees to masticate seagrasses. *Mar. Mamm. Sci.* **15**(1): 250-55.
- McKenzie, L. J., 1994. Seasonal changes in biomass and shoot characteristics of a *Zostera capricorni* Aschers dominant meadow in Cairns Harbour, northern Queensland. *Aust. J. Mar. Freshwater Res.* **45**: 1337-352.
- McNaughton, S. J., 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* **113**: 691-703.
- Mellors, J. E., 1991. An evaluation of a rapid visual technique for estimating seagrass biomass. *Aquat. Bot.* **42**: 67-73.
- Ogden, J. C., Robinson, L., Whitlock, K., Daganhardt, H. and Cebula, R., 1983. Diel foraging patterns in juvenile Green Turtles (*Chelonia mydas*) in St. Croix United States Virgin Islands. *J. Exp. Mar. Biol. Ecol.* **66**: 199-203.
- Poiner, I. R. and Peterken, C., 1995. Seagrasses. Pp. 107-17 in *State of the Marine Environment Report for Australia*, Technical Annex: 1 Great Barrier Reef Marine Park Authority, Townsville.
- Poiner, I. R., Walker, D. I. and Coles, R. G., 1989. Regional studies-seagrasses of Tropical Australia. Pp. 279-303 in *Biology of Seagrasses*. A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region ed by A. W. D. Larkum, A. J. McComb and S. A. Shepherd. Elsevier, Amsterdam.
- Preen, A., 1992. Interactions Between Dugongs and Seagrasses in a Subtropical Environment. Unpublished Ph.D. thesis, James Cook University, Townsville, Qld. V. I and II.

- Preen, A., 1995. Impacts of Dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Mar. Ecol. Prog. Ser.* **124**: 201-13.
- Preen, A. R., Lee Long, W. J. and Coles, R. G., 1995. Flood and cyclone related loss, and partial recovery, of more than 1 000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquat. Bot.* **52**: 3-17.
- Read, M. A., 1991. Observations on the Feeding Ecology of Immature Green Turtles *Chelonia mydas*, in the Moreton Banks Region of Moreton Bay, South-east Queensland. Honours thesis, University of Queensland, Brisbane.
- Reynolds, J. E. and Odell, D. K., 1991. Manatees and Dugongs. Facts on File, New York.
- Short, F. T., 1983. The response of interstitial ammonium in eelgrass (*Zostera marina*) beds to environmental perturbations. *J. Exp. Mar. Biol. Ecol.* **68**: 195-208.
- Supanwanid, C., 1996. Recovery of the seagrass *Halophila ovalis* after grazing by Dugong. Pp. 315-18 in *Seagrass Biology, Proceedings of an International Workshop, Rottneest Island, Western Australia, 25-29 January 1996* ed by J. Kuo, R. C. Phillips, D. I. Walker and H. Kirkman. Faculty of Science, University of Western Australia, Nedlands, Western Australia.
- Thayer, G. W., Bjorndal, K., Ogden, J., Williams, S. and Zieman, J., 1984. Role of the large herbivores in seagrass communities. *Estuaries* **7**: 351-76.
- Wake, J. A., 1975. A Study of the Habitat Requirements and Feeding Biology of the Dugong, *Dugong dugon* (Muller). Honours thesis, James Cook University, Townsville
- Zieman, J. C., Iverson, R. L. and Ogden, J. C., 1984. Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Mar. Ecol. Prog. Ser.* **15**: 151-58.