

Effects of simulated green turtle regrazing on seagrass abundance, growth and nutritional status in Moreton Bay, south-east Queensland, Australia

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Abstract. In some parts of their range, green turtles maintain grazing plots in seagrass beds by regular regrazing. The effects of simulated repeated grazing on subtropical seagrasses in Moreton Bay, Australia were investigated in a manipulative experiment over summer. Three seagrass species were subjected to two different clipping frequencies (simulating turtle cropping) and compared with unclipped controls over a 3.5-month summer period for the effects on seagrass biomass, leaf size and regrowth rates and water-soluble carbohydrate (WSC) and starch content. The order of the seagrass species' relative tolerance to simulated grazing was *Halophila ovalis* > *Zostera capricorni* > *Cymodocea serrulata*. Frequent regrazing of the green turtle's preferred seagrass, *H. ovalis*, resulted in an increase in leaf regrowth rate so that standing biomass of leaves and total plant material was maintained, suggesting an increase in productivity. Furthermore, whole-plant concentrations of WSC increased significantly in clipped *H. ovalis* plants relative to unclipped controls. In contrast, leaf biomass of the seagrass species less preferred by turtles, *Z. capricorni* and *C. serrulata*, decreased in response to repeated leaf removal relative to controls, despite maintenance of leaf regrowth rates. *C. serrulata* responded to repeated clipping with a reduction in leaf size and a decrease in rhizome WSC concentration. *Z. capricorni* also produced fewer and smaller new leaves. The ability of the preferred species, *H. ovalis*, to increase production of nutrient-rich standing crop in response to regrazing has major implications for green turtles and other seagrass grazers.

Additional keywords: *Chelonia mydas*, disturbance, green turtle, regrazing, seagrass.

Introduction

Plant productivity, distribution, community structure, nutrient relations and tissue nutrient content have all been demonstrably altered by the action of herbivores in terrestrial and algal-based marine systems (Thayer *et al.* 1984; Valentine and Heck 1991; Duffy and Hay 2001). However, herbivore–seagrass interactions have not been so well documented and the structural and functional responses of seagrass communities to grazing may be different to those of algae and terrestrial plants (Thayer *et al.* 1984; Valentine and Heck 1991). Effects of herbivory by large vertebrates on *Thalassia testudinum* have been studied in the Caribbean (e.g. Bjorndal 1980, 1985; Thayer *et al.* 1984; Zieman *et al.* 1984; Williams 1988) and the effects of grazing on *Zostera* species have been investigated in northern Europe (Jacobs *et al.* 1981) and North America (Buchsbaum and Valiela 1987). These studies have shown that grazing may alter the absolute and relative abundance of species in seagrass communities and also the physiology and morphology of individual seagrass plants. Despite the relative abundance of large vertebrate seagrass grazers in Australian waters, few studies have examined the effects of grazing on Australian seagrasses (e.g. Aragonés and Marsh 2000).

The green turtle, *Chelonia mydas* (Linnaeus, 1758), is the most abundant large vertebrate consumer of seagrasses in the

world (Ogden 1980) and there are significant populations of green turtles found in Australian waters (Limpus 1982). Moreton Bay in south-east Queensland is an important subtropical feeding ground for green turtles (Limpus *et al.* 1994), supporting an estimated population of ~10 000 animals (C. Limpus, pers. comm.). In this bay turtles graze regularly on five species of seagrass, with *Halophila ovalis* ostensibly the most important seagrass in the diet of both immature (Read 1991; Brand 1995; Brand-Gardner *et al.* 1999) and adult animals (Limpus *et al.* 1994). When green turtles graze on seagrasses, they remove a large proportion of the standing stock by cropping the leaf blades close to the sediment surface but do not disturb the underground rhizome system (Lanyon *et al.* 1989; Brand-Gardner *et al.* 1999). Close cropping in this way ensures that turtles reach the oval leaves of *H. ovalis*, which grow from a petiole less than two centimetres long. The size of the patch of seagrass leaves removed by individual grazing turtles appears to be small and variable in Moreton Bay, but in the order of <0.1 m², i.e. smaller than patches observed in feeding grounds elsewhere (Ogden *et al.* 1983).

In Moreton Bay, green turtles show a high degree of fidelity to feeding sites and their grazing is largely restricted to intertidal and shallow subtidal seagrass beds in the eastern bay (Read 1991; Brand 1995). Although there is no direct evidence that turtles

Table 1. Schedule for sampling cores and clipping samples
 Parentheses indicate number of days since previous clip. Sample times in bold indicate when cores were taken

Treatment	Time step and date							
	T0 14-Oct	T1 29-Oct	T2 12-Nov	T3 26-Nov	T4 10-Dec	T5 25-Dec	T6 8-Jan	T7 23-Jan
Control plots	Initial core (all plots)				Mid-term core (all plots)			Final core (all plots)
4-weekly plots	Initial core (all plots)	Clip		Clip (28)	Mid-term core (all plots)	Clip (29)		Final core (all plots) (29)
2-weekly plots	Initial core (all plots)	Clip	Clip (14)	Clip (14)	Mid-term core (all plots) and clip (14)	Clip (15)	Clip (14)	Final core (all plots) (15)

in this region maintain distinct feeding plots as they do in the Atlantic (Bjorndal 1980), the dense aggregations of feeding turtles suggest that regrazing of areas probably occurs. Such regrazing can potentially affect the absolute abundance of seagrass in the short term and the community composition of seagrass beds in the longer term. Seagrass removal and repeated regrazing at feeding plots (i.e. feeding philopatry) may also influence the physiology, chemistry and community composition of seagrasses at a local scale (Bjorndal 1980, 1985; Thayer *et al.* 1984; Aragonés 1996; Aragonés and Marsh 2000). Moreover, the bare patches in seagrass meadows caused by the selective grazing of turtles (Ogden *et al.* 1983; Read 1991; C. Limpus, pers. comm.) may be sufficiently common to cause small-scale changes in sedimentation and turbidity, which may in turn affect seagrass regrowth and recolonisation locally. These gaps created in seagrass meadows increase the 'edge' effect along which erosion may occur and the space available for seagrass regeneration via seed (Clarke and Kirkman 1989; Walker *et al.* 1989).

The objectives of the present study were to investigate the impacts of repeated simulated turtle cropping (i.e. clipping) on seagrass at small spatial and temporal scales and to investigate the physiological effects of regrazing on individual plants. In particular, we were interested in monitoring changes in absolute biomass of seagrasses within feeding patches, seagrass available to turtles, leaf size and regrowth rates and carbohydrate reserves during the summer months when grazing activity is highest. These parameters potentially influence both the recovery of seagrasses after grazing and the nutrition of green turtles and therefore patterns of regrazing activity.

Materials and methods

Study site

The study was conducted on Wanga Wallen Bank (27°25'S, 153°26'E) on the north-western side of North Stradbroke Island in eastern Moreton Bay, south-east Queensland, which supports 582 ha of seagrasses (Hyland *et al.* 1989). This site is unique in that it contains all six species of seagrasses that occur in Moreton Bay (Young and Kirkman 1975; Coles *et al.* 1989), five of which are utilised as food by green turtles in the bay (Read 1991). Although green turtles feed commonly on intertidal seagrass beds in Moreton Bay at high tide, adult turtles and dugongs are generally absent from this area because Wanga Wallen Bank is separated from the main seagrass banks by a channel (J. Lanyon, pers. obs.), whereas juvenile green turtles occur occasionally

(C. Limpus, pers. comm.). Accordingly, this site is well suited for the present work as our manipulations were unlikely to be confounded by interference from turtles and dugongs. Importantly, there was no evidence of extraneous grazing in any of our experimental plots.

Sampling design

A manipulative field experiment of 3.5-months duration over the peak-growing period of spring–summer (October–January inclusive) was conducted to determine the effect on seagrasses of repeated clippings (simulated turtle cropping) at different frequencies (Table 1). Since densities of feeding green turtles and dugongs are highest on the eastern banks over spring–summer (September to February inclusive), this is the time when the frequency of regrazing is likely to be greatest (Lanyon 2003).

A series of 1-m² experimental plots were positioned in a stratified random manner along a transect running perpendicular to the shore and along a depth gradient. The size of these plots was similar to, or in some cases slightly larger than, individual feeding patches created by green turtles in Moreton Bay (J. Lanyon, pers. obs.). The transect crossed three 'zones' comprising (i) a high intertidal area of mixed *Zostera capricorni* and *Halophila ovalis*, (ii) a mid-intertidal area of mixed *Z. capricorni* and *H. ovalis* and (iii) a subtidal monospecific stand of *Cymodocea serrulata*. Green turtles feed on *Zostera capricorni* and *H. ovalis* but not *C. serrulata* in Moreton Bay, in both intertidal and subtidal areas (Read 1991; Brand 1995).

Within each 'zone', there were three randomly positioned 1-m² replicate plots of each of three treatments, *viz.* unclipped controls and plots clipped at 2- and 4-weekly intervals, totalling 27 plots. Each plot was large enough to allow the removal of several cores (see below), which we assume to be independent, while avoiding edge effects. Corners of each plot were marked with labelled PVC pipe that protruded no more than 50 mm above the substratum.

Sample collection

At the start of the experiment, a single sediment core (diameter 148 mm, depth 150 mm) containing entire seagrass plants was taken from each plot to establish initial estimates of biomass, leaf morphometrics and carbohydrate levels (Time 0). Seagrass densities within zones were sufficiently homogeneous to enable density estimates from cores with acceptably low variances. Cores were taken again after 8 (Time 4) and 14 (Time 7) weeks to monitor responses to experimental clipping and/or seasonal

changes (yielding a total of 81 cores) (Table 1). Initial core samples were taken from the north-east quadrant of each plot, the mid-term core samples from the south-west quadrant and the final core from the centre of each plot. Cores were rinsed in fresh seawater and stored frozen until further processing. Holes resulting from the removal of cores were filled immediately and carefully with sand to prevent fish and invertebrates grazing on the newly severed and exposed roots and rhizomes (Zieman 1976) and/or the alteration of water-flow patterns over the plots.

Artificial clipping was used to imitate the natural methodical removal by green turtles of all leaf blades of seagrass within a feeding plot (after Ogden *et al.* 1983; Read 1991; Brand 1995). All seagrass species examined here had relatively short leaves. *H. ovalis* leaves and petioles extended less than 50 mm above the sediment, whereas the leaves of both *Z. capricorni* and *C. serrulata* were shorter than 150 mm and usually less than 100 mm in length. To simulate the natural cropping of seagrasses by green turtles (Read 1991; Brand 1995), seagrass shoots were clipped uniformly down to the level of the substratum over the entire area of each clipped plot, but without disturbing the underground rhizome system (Aragones and Marsh 2000). During clipping, leaf cuttings (clippings) from a central circular area within a diameter of 148 mm were retained for analysis. Clipping was conducted on the falling tide close to low tide so that cuttings not collected were removed by tidal flow soon after the manipulation. Leaves retained for analysis were stored frozen. At the end of the experiment, the central areas from which the clip samples had been collected previously were also cored (see above).

Sample processing

Seagrasses from cores were sorted into species and separated into plant parts. On each sampling occasion, leaf widths of *C. serrulata* and *Z. capricorni*, and leaf lengths of *H. ovalis*, were measured to assess changes in leaf size in response to clipping. Leaf length rather than width was measured for the oval-shaped leaves of *H. ovalis* since this dimension varies most markedly between individual plants. Plant parts were dried at 60°C to constant dry weight. These weights formed the basis of estimates of biomass of above-ground (leaves) and below-ground (rhizomes, roots) parts and community composition. Dried samples for WSC and starch analyses were milled to fine powder in a Retsch ball-mill (Retsch, Haan, Germany) and stored in air-tight vials.

Leaves clipped from the centre of plots were rinsed, sorted into species and dried at 60°C to constant weight. The biomass of these clippings was added to leaf weights from the final central cores for each plot to estimate the total amount of leaves available during the experimental period (see below).

Estimating seagrass biomass, growth and storage products

Total biomass (expressed as g m^{-2} dry weight) of each species in the cores was estimated by summing the weights of the separated leaves, roots and rhizomes. We also considered the biomass of the separate plant parts for each species.

Above-ground biomass produced per unit area available to grazers over the experimental period was estimated as the summed weights of leaf clippings that grew after the initial clip, added to the leaf biomass from the final cores taken from the

clipped plots (at Time 7). For the 4-weekly and 2-weekly clip regimes, the biomass per unit area of leaves from the final core was added to that collected after 2 and 5 clippings respectively.

To estimate the extent to which simulated grazing stimulated production of above-ground biomass available to grazers, the amount of leaf material produced in the clipped plots was compared with that produced in control plots. Because the controls were not clipped, the amount of leaf material produced was estimated as leaf biomass in the final cores minus leaf biomass from the initial cores. The significance of this difference was examined using paired *t*-tests for each species. Note that in interpreting these measures, our focus is on leaf material that is available to grazers. It is not necessary to assume zero losses of leaves to detritus over the relatively short experimental period, although we do assume that losses to other grazers are negligible.

The daily rate of leaf regrowth was estimated from the weight of leaf clippings collected from regrowth intervals between subsequent clips, divided by the number of days of regrowth (Table 1). Regrowth rates in plots clipped at 4-weekly intervals were based on the weights of clippings collected at Times 3 and 5 (28- and 29-day regrowth periods respectively), whereas in plots clipped at 2-weekly intervals, regrowth rates were based on clippings collected at Times 2 and 6 (both 14-day regrowth periods) (Table 1). Although the final core samples also represented a period of regrowth, these were not used because the collection method for leaf biomass was different, i.e. cored rather than clipped.

Initial and final core samples of each seagrass species were analysed for WSCs. For *Z. capricorni* and *C. serrulata*, the carbohydrate content of leaves, roots and rhizomes was determined separately, whereas it was necessary to pool plant parts of *H. ovalis* because of its small biomass. Total soluble carbohydrates were analysed using Jermyn's (1975) modification of the anthrone method (Yemm and Willis 1954). Starch content of the rhizomes of each species was determined on the residue after soluble carbohydrate extraction (Total Starch Assay Procedure, TSA9/92, Megazyme, Wicklow, Ireland).

Statistical analysis

All analyses were undertaken using the SAS software package (SAS, Cary, NC). Since initial analyses indicated that the factor 'zone' was not significant ($P > 0.25$ in all cases), data from samples across the depth transect were pooled for the final analyses. The responses of the three seagrass species to the clipping treatments were examined by factorial Model I ANOVAs. To examine the significance of differences in responses among seagrass species, clipping treatments and times (all fixed effects), separate 3-way ANOVAs were run for each of nine parameters (1, total biomass; 2, leaf biomass; 3, rhizome biomass; 4, relative abundance of species based on total biomass; 5, relative abundance of species based on standing crop (above-ground fraction); 6, leaf regrowth after two growth intervals; 7, leaf size (for each species separately); 8, WSC content; and 9, starch content). Before ANOVA, the relationships between treatment group means and standard deviations were examined to assess homoscedasticity and determine the appropriate transformation to stabilise the variances when required (after Draper and Smith

1981). Transformations are expressed in terms of the untransformed variate, Y . Normality of residuals was assessed from normal probability plots, and the Shapiro–Wilk W -statistic. In all cases, after transformations, residuals were distributed normally and the variances were sufficiently homogeneous so that data met the assumptions of ANOVA. The nature of ‘treatment’ effects indicated by significant overall tests were determined by *a posteriori* Ryan–Einot–Gabriel–Welsch (REGWQ) multiple comparison tests.

Different parts of the same plants of *C. serrulata* and *Z. capricorni* were analysed for WSCs. However, for any particular plant, the different plant parts (leaves, rhizomes, roots) are not independent. Accordingly, we analysed these data using two ANOVA models: (i) a standard 4-way Model I ANOVA on factorial combinations of seagrass species, time, treatment and plant part (all fixed effects) where any correlations among different parts of the same plant were ignored; and (ii) a ‘complete’ analysis, which included an additional random effect to account for individual plants (where ‘plant’ is nested within combinations of species \times time \times treatment). The latter analysis lacks replication because there can only be one individual of a particular plant. Results of these two analyses for the effects of interest (i.e. species, time, treatment, plant part and all possible interactions of these effects) were qualitatively identical at the level of $\alpha = 0.05$, suggesting that any ‘plant’ effect was weak and that the data were effectively behaving independently. Results of the complete model analysis are included here. Thus, to interpret the multiway interactions indicated by the complete model (these results are presented in Table 2), we used *post hoc* REGWQ multiple range tests conducted on the data where we ignore plant effect. A separate 2-way ANOVA was used to examine the significance of treatment and time effects on WSC levels in whole plants of *H. ovalis*, because samples of this species were too small to examine differences between different plant parts.

Results

Leaf size

Clipping treatments did not significantly affect leaf length in *H. ovalis* ($F_{2,34} = 1.52$, $P = 0.234$) (Table 2). However, clipping led to a significant decrease in the width of regrown leaves in both *Z. capricorni* and *C. serrulata*. Over the course of the experiment, the leaf width of *Z. capricorni* increased in control plots (mean increase $\sim 30\%$ from 1.51 ± 0.18 to 1.96 ± 0.22 mm) but decreased in response to 4-weekly (mean decrease of 18.4% from 1.85 ± 0.17 to 1.51 ± 0.08 mm) and 2-weekly (mean decrease of 16% from 1.63 ± 0.16 to 1.36 ± 0.09 mm) clipping, indicated by a significant time \times treatment interaction ($F_{4,45} = 3.1$, $P = 0.025$). There was also a significant time \times treatment interaction for leaf width of *C. serrulata* ($F_{4,18} = 4.45$, $P = 0.011$). By the end of the clipping experiment, leaf widths in control plots had increased slightly (from 6.2 ± 0.25 to 6.4 ± 0.09 mm: a mean increase of 3.2%), whereas leaf widths decreased significantly in response to clipping. Mean width of leaves subjected to 4-weekly clipping decreased from 6.2 ± 0.13 to 5.5 ± 0.19 mm (a mean decrease of 11.3% , but which was not significant, REGWQ $P > 0.05$), whereas 2-weekly clipped leaves decreased significantly from 6.4 ± 0.3 to 5.3 ± 0.16 mm (mean decrease of 17.0% , REGWQ $P < 0.05$).

Total plant biomass

Seagrass species varied in their total biomass per unit area in the different clipping treatments (species \times time \times treatment interaction $F_{4,64} = 2.84$, $P = 0.03$) (Fig. 1, Table 2). The differences in the total biomass of each species before clipping simply reflect size differences among species, i.e. that *H. ovalis* is much smaller than the other two species and that *Z. capricorni* is smaller than *C. serrulata*. Three distinct trends were apparent with respect to biomass change of the three species (Fig. 1): (1) total biomass of *C. serrulata* decreased significantly (REGWQ $P < 0.05$) in response to clipping (Fig. 1a); (2) total biomass of *Z. capricorni* did not decrease significantly in response to clipping, although there was a non-significant trend towards a decrease (REGWQ $P > 0.05$; Fig. 1b); and (3) for *H. ovalis*, despite losses of plant material due to simulated grazing, the total plant biomass of *H. ovalis* after clipping was greater than that before commencement of grazing, although again this trend was not significant (REGWQ $P > 0.05$) (Fig. 1c).

Over the experimental period, mean total biomass of *C. serrulata* decreased in the control plots by a mean of 40.7% (from 403.63 ± 35.2 to 239.23 ± 8.42 g dry matter (dm) m^{-2}). Each of the clip treatments led to further decreases in total biomass of 67% : 4-weekly clipping decreased mean biomass by 188.64 g m^{-2} (from 208.2 ± 53.9 to 91.56 ± 26.7 g dry matter m^{-2}); and 2-weekly clipping decreased biomass by 154.07 g m^{-2} (from 230.93 ± 15.89 to 76.86 ± 20.83 g dm m^{-2}) (Fig. 1a). In contrast, mean total biomass of *Z. capricorni* increased in the control plots on average by 37% (from 116.2 ± 22.51 to 159.43 ± 26.43 g dm m^{-2}), but decreased by 42% (from 154.53 ± 18.97 to 89.85 ± 10.85 g dm m^{-2}) and 40% (from 136.6 ± 15.15 to 83.25 ± 8.12 g dm m^{-2}) as result of 4-weekly and 2-weekly clipping respectively (Fig. 1b).

Leaf biomass

There were significant differences in how the different seagrass species responded to the treatments in terms of standing leaf biomass (species \times treatment \times time $F_{8,100} = 3.43$, $P = 0.0016$) (Table 2; Fig. 2).

Clipping treatments appeared to increase the amount of leaf biomass of *H. ovalis*, although the trend was not significant (REGWQ $P > 0.05$; Fig. 2c). In contrast, clipping resulted in significant decreases in standing leaf biomass per unit area for both *C. serrulata* and *Z. capricorni* (REGWQ $P < 0.05$). For *Z. capricorni*, 4-weekly clipping reduced leaf biomass by 71% (from 30.75 ± 1.4 to 8.95 ± 1.36 g dm m^{-2}) and 2-weekly by 88% (from 22.58 ± 5.94 to 2.7 ± 0.45 g dm m^{-2}) (Fig. 2b). This decline was also pronounced in *C. serrulata*, for which 4-weekly clipping resulted in a 79% decline in leaf biomass (from 72.9 ± 10.14 to 15.5 ± 5.79 g dm m^{-2}) and 2-weekly clipping brought about a highly significant 95% decline (from 95.3 ± 6.06 to 4.63 ± 2.07 g dm m^{-2}) (Fig. 2a). Between 35 and 40% of *C. serrulata* biomass comprised leaf material. Under frequent clipping, this standing crop declined by 95% .

Rhizome biomass

The seagrass species showed different responses to the clipping treatments in terms of rhizome biomass (species \times treatment $F_{4,99} = 2.67$, $P = 0.037$) (Table 2). Rhizome biomass per unit

Table 2. Summary table of ANOVA results for effects of 2-weekly and 4-weekly clipping treatments on various parameters of all three seagrass species (*Cymodocea serrulata*, *Zostera capricorni* and *Halophila ovalis*) unless otherwise statedWSC, water soluble carbohydrates; C, clipping treatment; T, time; S, species; P, plant part; ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Dependent variable	Transformation	Source	d.f.	F	P	Significance
Leaf size						
<i>H. ovalis</i>	ln(Y)	C × T	4, 34	1.53	0.216	ns
		C	2, 34	1.52	0.234	ns
<i>Z. capricorni</i>	Y ^{1.41}	C × T	4, 45	3.1	0.025	*
<i>C. serrulata</i>	None	C × T	4, 18	4.45	0.011	*
Total plant biomass density	Y ^{0.125}	S × T × C	4, 64	2.84	0.03	*
Leaf biomass density	Y ^{0.292}	S × T × C	8, 100	3.43	0.0016	**
Rhizome biomass density	Y ^{0.13}	S × T × C	8, 99	1.34	0.23	ns
		S × C	4, 99	2.67	0.037	*
		C × T	4, 99	0.5	0.734	ns
Root biomass density	Y ^{0.177}	S × T	4, 99	5.34	0.0006	***
		S × T × C	8, 100	0.68	0.707	ns
		S × C	4, 100	1.8	0.136	ns
		C × T	4, 100	0.59	0.673	ns
		S × T	4, 100	6.28	0.0001	***
Leaf production	Y ^{0.25}	S × C	2, 24	0.02	0.982	ns
		S	2, 24	34.06	0.0001	***
		C	1, 25	6.22	0.019	*
Leaf regrowth rate	Y ^{0.14}	S × T × C	2, 48	1.44	0.247	ns
		S × C	2, 48	0.28	0.755	ns
		C × T	1, 48	0.63	0.432	ns
		S × T	2, 48	1.88	0.164	ns
		S	2, 48	66.15	0.0001	***
		C	1, 48	6.44	0.014	*
		T	1, 48	2.32	0.134	ns
WSC	ln(Y)					
<i>Z. capricorni</i> & <i>C. serrulata</i>		S × T × C × P	4, 84	0.89	0.471	ns
		S × T × C	2, 84	1.22	0.306	ns
		S × C × P	4, 84	1.56	0.193	ns
		S × T × P	2, 84	8.57	0.0004	***
		T × C × P	4, 84	5.63	0.0005	***
<i>H. ovalis</i>		C × T	2, 17	1.79	0.209	ns
		C	2, 17	4.06	0.045	*
		T	1, 17	24.28	0.001	***
Starch	Y ^{0.4}					
<i>Z. capricorni</i> & <i>C. serrulata</i>		S × T × C	2, 42	1.5	0.235	ns
		S × C	2, 42	7.07	0.002	**
		C × T	2, 42	0.35	0.705	ns
		C × T	1, 42	0.06	0.814	ns

area of *Z. capricorni* and *H. ovalis* did not change significantly (REGWQ $P > 0.05$) in response to clipping treatments. In contrast, *C. serrulata* rhizome biomass tended towards a decrease for all treatments, but this decrease was only significant (REGWQ $P < 0.05$) under the 2-weekly clip regime when biomass dropped by a mean of 45.1%, i.e. from 104.7 ± 3.84 to 59.56 ± 15.42 g dm⁻². This was reflected in the species × time interaction ($F_{4,99} = 5.34$, $P = 0.0006$).

Root biomass

Root biomass of the three seagrass species was not affected by the clipping treatments (species × time × treatment $F_{8,100} = 0.68$, $P = 0.707$; species × treatment $F_{4,100} = 1.8$, $P = 0.136$; time × treatment $F_{4,100} = 0.59$, $P = 0.673$; treatment

$F_{2,100} = 0.75$, $P = 0.475$) (Table 2). The only significant interaction was species × time ($F_{4,100} = 6.28$, $P = 0.0001$) and this reflected both the lower biomass of *H. ovalis* root material present compared to the other species at each sampling time irrespective of treatment and relatively greater decline in root biomass of *H. ovalis* over the experimental period compared with the other species' declines.

Above-ground biomass available to grazers

By collecting the leaves between successive clippings it was possible to calculate above-ground biomass produced and available to grazers over the 3-month period 29 October–23 January (Fig. 3). Above-ground biomass was clearly influenced by both species and clipping treatment (2-way

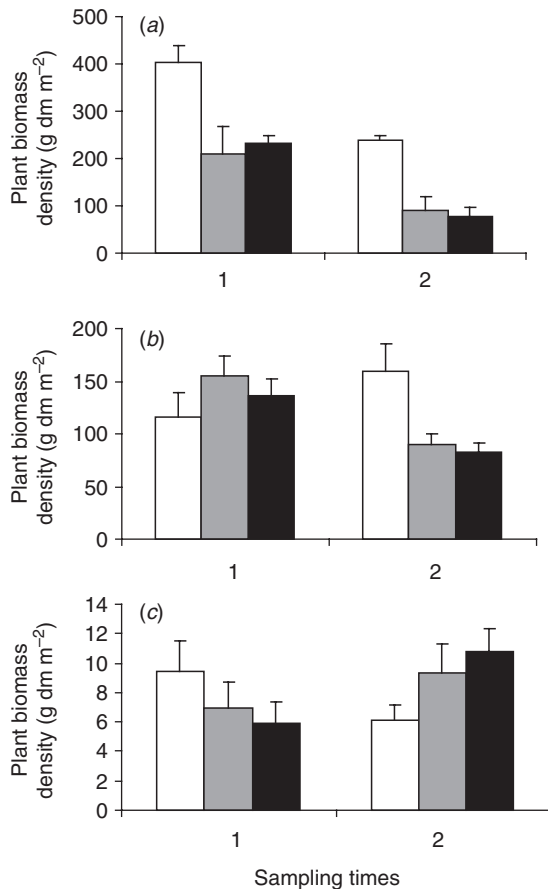


Fig. 1. Changes in total plant biomass density (mean \pm s.e. g dry matter m^{-2}) in control (open bars), 4-weekly (grey bars) and 2-weekly (black bars) clip treatment plots over the experimental period for (a) *Cymodocea serrulata*, (b) *Zostera capricorni* and (c) *Halophila ovalis*. Time 1 = initial core, Time 2 = final core.

ANOVA: species, $F_{2,24} = 34.06$, $P < 0.0001$; clipping treatment, $F_{1,24} = 6.22$, $P = 0.019$; species \times treatment, $F_{2,24} = 0.02$, $P = 0.982$ (Table 2). Above-ground biomass per unit area resulting from *Z. capricorni* and *C. serrulata* were similar ($P > 0.05$, REGWQ), but both were significantly greater than the absolute rates of production of new leaf material in *H. ovalis* ($P < 0.05$). Notably, irrespective of species, above-ground biomass in plots subject to 2-weekly clipping was significantly greater than that in plots clipped every 4 weeks (Fig. 3). In control plots not subjected to clipping, the leaf biomass available to grazers at the beginning of the experiment was not significantly different to that at the end for *C. serrulata* and *H. ovalis*, paired t -tests: $t_2 = -0.923$, $P = 0.453$ and $t_5 = -1.229$, $P = 0.274$ respectively, whereas the amount of leaves of *Z. capricorni* increased on average by 24.2 g dm^{-2} in control plots, which is highly significant, paired t -test, $t_5 = 5.00$, $P = 0.004$. Thus, although the entire production of available biomass of leaves of *C. serrulata* and *H. ovalis* can be attributable to stimulated growth as a result of clipping, for *Z. capricorni* only 66.7% and 53.0% of production in the 2- and 4-weekly clipped plots respectively can be attributable to stimulation by clipping.

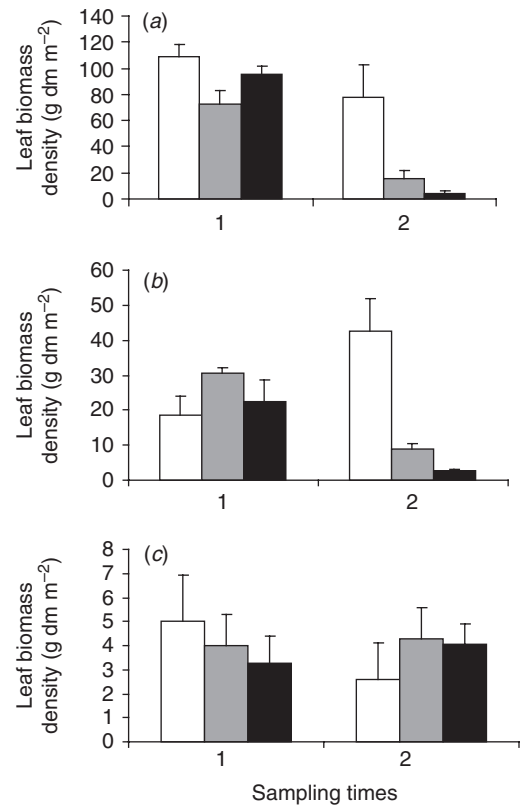


Fig. 2. Changes in leaf biomass density (mean \pm s.e. g dry matter m^{-2}) in control (open bars), 4-weekly (grey bars) and 2-weekly (black bars) clip treatment plots over the experimental period for (a) *Cymodocea serrulata*, (b) *Zostera capricorni* and (c) *Halophila ovalis*. Time 1 = initial core, Time 2 = final core.

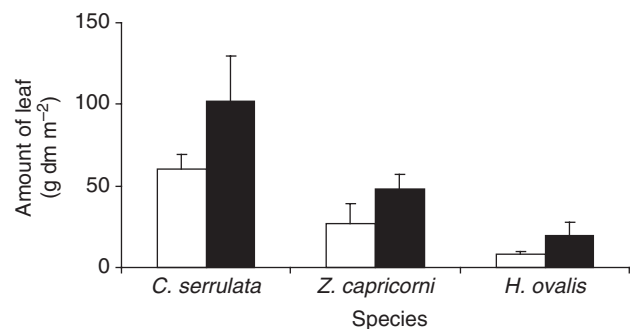


Fig. 3. Amount of leaf (mean \pm s.e. g dry matter m^{-2}) produced by 4-weekly (open bars) and 2-weekly (solid bars) clip treatments over the experimental period (between 29 October and 23 January) for *Cymodocea serrulata*, *Zostera capricorni* and *Halophila ovalis*. Note that leaf production is net gain or loss and has been adjusted according to any gain or loss in the control plots.

Rates of leaf regrowth

Leaf regrowth rates differed significantly between species (effect of species: $F_{2,48} = 66.15$, $P = 0.0001$) (Table 2). Mean leaf regrowth rates of *H. ovalis* ($0.097 \pm 0.011 \text{ g day}^{-1}$) were significantly lower (REGWQ $P < 0.05$) than that

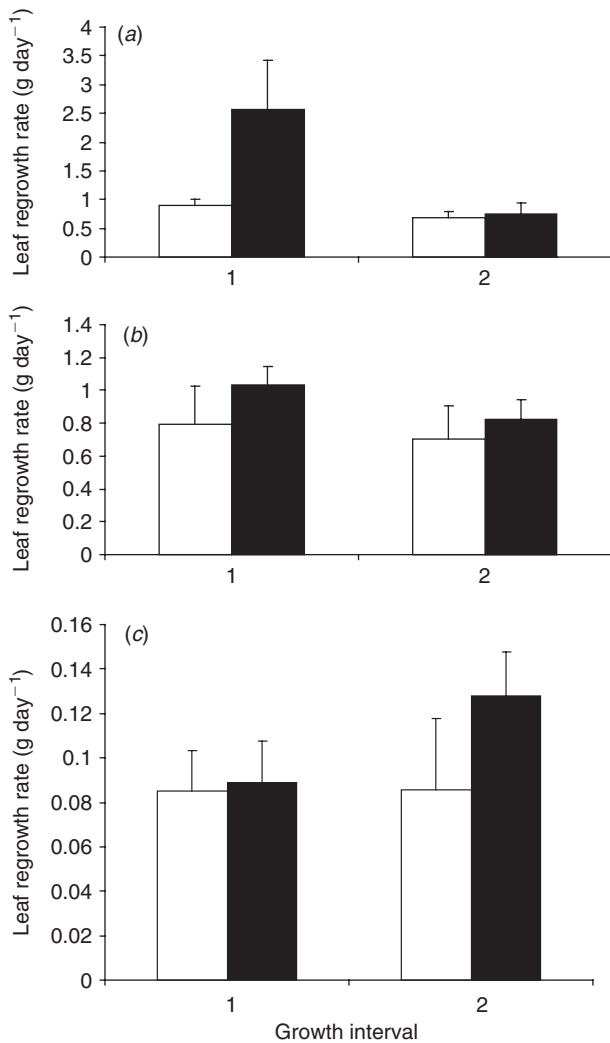


Fig. 4. Leaf regrowth rates (mean \pm s.e. g day⁻¹) of (a) *Cymodocea serrulata*, (b) *Zostera capricorni* and (c) *Halophila ovalis* produced by 4-weekly (open bars) and 2-weekly (solid bars) clip treatments over two growth intervals.

of *Z. capricorni* (0.838 ± 0.085 g day⁻¹) and *C. serrulata* (1.224 ± 0.301 g day⁻¹), whereas the difference in regrowth rates of the latter two species was not significant. This pattern was independent of the rate of simulated grazing. Notably, in all species, leaf regrowth rates were significantly higher in plots in which simulated grazing occurred every 2 weeks than in plots grazed at 4-weekly intervals ($F_{1,48} = 6.44$, $P = 0.015$; Fig. 4). There were no significant interaction effects (Table 2).

Water-soluble carbohydrates (WSCs)

There were complex interactions among effects of seagrass species, plant part, clipping treatment and 'time' (i.e. before v. after clipping treatments) on WSC content. Although the 4-way interaction was not significant, the 3-way interactions of plant part \times time \times species and plant part \times time \times treatment were highly significant (Tables 2, 3). The interaction among effects of plant part \times time \times species indicates that differences

among plant parts depended on the species and whether the plants were assessed at the beginning or end of the experiment. Although levels of WSC were similar in all plant parts of *Z. capricorni* both at the beginning and end of the experiment, in *C. serrulata* the WSC content of rhizomes was much higher than in the roots and, in particular, the leaves and these differences were more pronounced before instigation of the clipping treatments (Table 3). This effect reflects that in *C. serrulata*, on average, the relatively low WSC content of the leaves increased over the course of the experiment, whereas the high levels of WSC in the rhizomes tended to decrease. Overall, the WSC content of all plant parts of *C. serrulata* was higher than that of *Z. capricorni*.

The significant plant part \times time \times treatment interaction reflects that differences between plant parts in WSC across both species depended on both the clipping treatment and whether the assays were taken before or after the treatments. This interaction highlighted that although the WSC content of rhizomes was higher than in the other plant parts in all treatments, after clipping the WSC content declined in rhizomes but tended to increase in leaves. In contrast, in the controls (not subject to simulated grazing), in all plant parts WSC levels were similar at the beginning and end of the experiment. Simulated grazing had no effect on WSC levels in the roots.

The concentration of WSC in whole plants of *H. ovalis* (it was not possible to analyse the separate plant parts) differed significantly between treatments ($F_{2,17} = 4.06$, $P = 0.045$) and between times ($F_{1,17} = 24.3$, $P < 0.001$). The WSC content of *H. ovalis* increased as the frequency of clipping increased so that seagrasses clipped at 2-weekly intervals had significantly higher (REGWQ $P < 0.05$) mean concentrations of WSC (46.3 ± 8.3 mg g⁻¹ dm) than the less frequently clipped 4-weekly clip plots (26.3 ± 1.7 mg g⁻¹ dm) (Table 3). Further, the concentrations of WSC approximately doubled over the course of the experiment in all control and treatment plots of *H. ovalis* (from 18.7 ± 2.2 mg g⁻¹ dm to 38.4 ± 4.4 mg g⁻¹ dm (REGWQ $P < 0.05$)).

Starch

No starch was detected in whole-plant samples of *H. ovalis*. In contrast, starch was measurable in the rhizomes of both *C. serrulata* and *Z. capricorni*. The starch levels in these two species responded differently with respect to the clipping treatments (species \times treatment $F_{2,42} = 7.07$, $P = 0.002$). Clipping did not affect starch levels in rhizomes of *C. serrulata*, but caused a significant decrease (REGWQ $P < 0.05$) in *Z. capricorni*, particularly at the highest clipping frequency. The mean starch level in *Z. capricorni* rhizomes dropped by 35% from 6.63 ± 0.94 mg g⁻¹ dry matter in controls to 4.29 ± 0.42 mg g⁻¹ dm under the 4-weekly clipping treatment and by 57% to 2.82 ± 0.29 mg g⁻¹ dm when subject to clipping at 2-weekly intervals.

Discussion and conclusion

Simulated turtle regrazing (leaf clipping) over 3.5 months during summer affected the production and standing biomass of leaves available to grazers, leaf morphology and the chemical composition of seagrasses. The magnitude of the response to this disturbance depended on the seagrass species and, in some

Table 3. Water soluble carbohydrate content (WSC as % dry matter; mean \pm s.e.) of *Halophila ovalis*, *Cymodocea serrulata* and *Zostera capricorni* before (Time 1: October) and after (Time 2: January) clipping treatments

Treatments are control (no clipping), 4-weekly clipping and 2-weekly clipping. For *C. serrulata* and *Z. capricorni*, WSC leaves and rhizomes were analysed separately for WSC content, whilst for *H. ovalis* plant parts were not analysed separately

Species	Plant part	Control	Treatment		
			4-weekly	2-weekly	
<i>H. ovalis</i>	Whole plant	Time 1	14.6 \pm 1.4	16.7 \pm 0.9	26.3 \pm 1.7
		Time 2	42.7 \pm 6.6	26.3 \pm 1.7	46.3 \pm 8.3
<i>C. serrulata</i>	Leaves	Time 1	14 \pm 1.7	18 \pm 2.5	16.7 \pm 3.5
		Time 2	19 \pm 4	30.3 \pm 0.7	38.3 \pm 6.9
<i>C. serrulata</i>	Rhizomes	Time 1	132 \pm 12.3	119.7 \pm 18.6	116.7 \pm 14.1
		Time 2	65.7 \pm 8.2	77.3 \pm 16.4	139 \pm 22.9
<i>Z. capricorni</i>	Leaves	Time 1	14.8 \pm 1.2	8.5 \pm 0.4	11.5 \pm 1.3
		Time 2	12.3 \pm 2.0	18.3 \pm 2.7	18.8 \pm 1.9
<i>Z. capricorni</i>	Rhizomes	Time 1	12.2 \pm 2.7	11.8 \pm 1.8	9 \pm 1.3
		Time 2	19.7 \pm 2.2	14.2 \pm 2.3	14.5 \pm 2.4

cases, on the frequency of regrazing. These effects, as detailed below, are likely to occur in naturally grazed situations.

Seagrass biomass

Seagrass species varied in their responses to simulated grazing. In 'grazed' plots, the total standing plant biomass of *Cymodocea serrulata* and *Zostera capricorni* declined, whereas the biomass of *Halophila ovalis* was maintained over the course of the experiment. *Halophila ovalis* compensated for losses from grazing through enhanced production.

Despite the fact that clipping stimulated above-ground biomass produced in all species, simulated turtle regrazing resulted in a 40%+ reduction in whole-plant biomass of both *C. serrulata* and *Z. capricorni* over the course of the experiment. The magnitude of this decline was greater for *C. serrulata* than for *Z. capricorni*, particularly in the treatment with the highest frequency of grazing, suggesting that *C. serrulata* is less tolerant of this level of grazing pressure. The major source of this decline was a reduction in above-ground standing crop, reflecting both leaf removal and an inability of these species to regenerate leaves at a rate sufficient to maintain standing crop per unit area. At least part of this decline in leaf material was probably accounted for by a decrease in the size of new leaves, because leaf width decreased significantly in both species under the most frequent (2-weekly) clipping treatment. Another component of the decline in total plant biomass of *C. serrulata* was a reduction of \sim 45% in rhizome biomass. In contrast, *Z. capricorni* may allocate more resources to repair of rhizomes than to leaves when leaves are clipped (Bell and Westoby 1986). Clipping induced no detectable changes in root biomass of either species.

In contrast, *H. ovalis* showed no declines in either leaf biomass or leaf size despite regular leaf clipping. Total plant, leaf, rhizome and root biomass densities were all maintained. Moreover, with regrazing occurring every 2 weeks, total plant biomass

and standing crop did not increase significantly although there was a non-significant trend towards an increase, suggesting that sustained regrazing at this frequency may not only lead to maintenance of standing crop but to an increase in standing crop over the longer term through enhanced production. The rate of leaf regrowth increased significantly relative to controls with 4-weekly grazing and increased by a further \sim 50% when the frequency of grazing doubled to 2-weekly. This high specific growth rate under grazing pressure is consistent with *H. ovalis* being an opportunistic, pioneer species (den Hartog 1970; Clarke and Kirkman 1989; Lee Long *et al.* 1993). Similar increases in standing crop of *H. ovalis* have resulted from increasing spatial intensity (c.f. frequency or 'temporal intensity') of simulated grazing (Preen 1992; Aragones and Marsh 2000).

The maintenance of the biomass of leaves of *H. ovalis* available to grazers in the face of repeated leaf clipping reflects the significant increase in above-ground biomass per unit area. This response suggests that, at least at this time of the year, *H. ovalis* can more efficiently re-allocate its reserves into production of new leaves than *C. serrulata* and *Z. capricorni*. Because the period over which the experiment was conducted coincided with the period of peak summer growth of *H. ovalis*, but was after the winter-spring growth period for *Z. capricorni* and spring growth of *C. serrulata*, conducting the work in a different season may have yielded different results. However, since turtle grazing is most prevalent over the summer months (Brand-Gardner *et al.* 1999), our choice of timing is appropriate to address effects of turtle grazing.

Seagrass community composition

Since the standing crop of leaves of *H. ovalis* recovered rapidly after clipping, even increasing with clipping at 2-weekly intervals, while the standing biomass of *Z. capricorni* leaves was reduced at both levels of clipping, then in the mixed *H. ovalis*

and *Z. capricorni* beds, our simulated turtle regrazing effectively realised a shift in seagrass community composition in the above-ground component. This finding is consistent with other work that has examined the effects of different spatial intensities of simulated grazing on meadows with similar species compositions. Aragones and Marsh (2000) found that a tropical meadow dominated by *Z. capricorni* shifted in community composition in favour of *H. ovalis* after a single bout of simulated turtle grazing. Preen (1992) reported a similar community change in Moreton Bay, but only in his most intensively grazed treatment in which 90–95% of the seagrass was removed.

Aragones and Marsh (2000) suggested that changes in community composition may depend in part on the seasonal growth patterns of the component seagrass species. Our experiment was conducted over the summer period during the peak growing season for *H. ovalis* so that its leaf regrowth rates might be expected to be close to maximum. In contrast, the winter–spring growth flush of *Z. capricorni* in Moreton Bay had passed by the start of this experiment so that the regrowth capacity of *Z. capricorni* may have been relatively depressed.

No change in species composition was recorded during simulated regrazing of the monospecific *C. serrulata* meadow in that no other seagrass species colonised the areas denuded by leaf clipping. This is possibly because the thick rhizomes and roots of *C. serrulata* (Poiner 1984) present just beneath the sediment surface make it difficult for sporelings of other species to invade. In some areas of Moreton Bay, *C. serrulata* has been observed to inhibit colonisation by *Z. capricorni* (Poiner 1984). Moreover, the short time frame of the present study was probably not long enough for colonisers to establish. With simulated regrazing, leaf biomass of *C. serrulata* was significantly reduced. In fact, the condition of *C. serrulata* deteriorated so rapidly in plots where simulated grazing had been most frequent, that by the end of this experiment grazed areas were noticeably degraded, with a 95% decrease in leaf biomass resulting in mostly bare sediment. This experiment indicates that *C. serrulata* is intolerant to this level of grazing pressure, particularly during the summer months when its growth rates are low. *C. serrulata* in Moreton Bay follows a bimodal seasonal pattern, with biomass maxima occurring in October and April and minima in December and June (Young and Kirkman 1975). Furthermore, if *C. serrulata* in Moreton Bay is a tropical species at its southern limit (Boon *et al.* 1986; Clarke and Kirkman 1989), its tolerance to disturbance (e.g. grazing) may be relatively poor in this part of its range.

Carbohydrate content

Rhizomes have been identified as the principal storage organs for soluble carbohydrate reserves in seagrasses (Greenway 1974; Dawes and Lawrence 1983; Dawes *et al.* 1987; Lanyon 1991). WSC concentrations (i.e. sugars) in rhizomes of *C. serrulata* were the highest of any species or plant part analysed in this study, and averaged about five times the levels found in its leaves and three times that in its roots. Similar concentration gradients of soluble carbohydrates, decreasing from rhizomes to leaves and roots, have been recorded in several genera of seagrasses (Drew 1980). In contrast, WSC levels in *Z. capricorni* were similar across plant parts during the present study period. We do not have data demonstrating relative WSC concentrations in component

parts of *H. ovalis*. However, other studies have documented relatively higher concentrations of WSC in the underground organs of *Halophila* compared with the leaves (Drew 1980; Dawes *et al.* 1987; Lanyon 1991) or similar levels in both leaves and rhizomes and/or roots (Aragones 1996).

Simulated regrazing led to changes in WSC concentrations in all three of the seagrass species examined. There was a significant increase in total WSC content of *H. ovalis* plants with increasing frequency of grazing. This increasing rate of WSC production may be linked with the presumed increase in rate of photosynthesis that is likely to occur with the increase in leaf growth rates and resultant standing crop. Altered growth rates have been found to affect the levels of soluble carbohydrates in seagrasses (Dawes *et al.* 1979), as well as their distribution between the leaves, rhizomes and roots (Dawes and Lawrence 1983). Drew (1980) found exceptionally high sucrose levels in the rhizomes of *H. ovalis* (corrected dry weight of 44%), compared with *C. serrulata* (4.3%) and *Z. capricorni* (7.8%). That starch levels were undetectable in *H. ovalis* suggests that the bulk of soluble carbohydrates were sugars. Further, the lack of starch granules in *H. ovalis* is consistent with low levels of storage carbohydrates present in other seagrass species during times of active leaf growth, e.g. during the peak growing season (Ott 1980; Pirc 1985). Presumably such mobilisation of these reserves also occurs under regrazing pressure. This high sucrose content of *H. ovalis* rhizomes may enhance the ability of this species to survive and recover from repeated and prolonged grazing by turtles. Furthermore, the increase in total WSC levels of grazed *H. ovalis* will provide a higher availability of soluble sugars to grazers including green turtles.

In *C. serrulata* and *Z. capricorni*, WSC levels altered in different ways in different plant parts in response to regrazing. In *Z. capricorni*, increasing the frequency of leaf clipping did not significantly alter the WSC concentrations in any plant part. However, trend but non-significant increases in WSC concentrations in both leaf and root fractions of *Z. capricorni* suggests that sustained regrazing (i.e. over a longer period than this experiment) may lead to significant effects. This trend may have resulted from mobilisation of starch reserves from the rhizomes of *Z. capricorni* during leaf regrowth. Starch concentrations in the rhizomes decreased significantly at the same time as WSC levels increased in other plant parts.

In contrast, there was a significant decrease in WSC in rhizomes of *C. serrulata* relative to other plant parts with increasing intensity of grazing, and a concomitant (but non-significant) rise in WSC concentrations in young leaves. This suggests that translocation of WSC from rhizomes to leaves was occurring during production of new leaves. Clipping did not affect rhizomatous starch reserves of *C. serrulata*.

Implications for herbivores

Simulated turtle cropping of three seagrass species in Moreton Bay indicated their relative tolerance to frequent regrazing over the summer period as *Halophila ovalis* > *Zostera capricorni* > *Cymodocea serrulata*. Notably, regrazing improves the abundance and nutrient content of *H. ovalis*, which is the preferred seagrass species of green turtles and dugongs in Moreton Bay.

When *H. ovalis* leaves are cropped repeatedly, rates of above-ground biomass produced increase so that leaves are regenerated rapidly, maintaining their biomass and that of the whole plant. Moreover, plant concentrations of WSCs (sugars) are increased. Soluble carbohydrate levels in seagrass leaves probably affect the quality of seagrass as a food source for turtles as they do in terrestrial pastures (Humphreys 1989; Jones and Roberts 1991; Radojevic *et al.* 1994). In addition, simulated turtle cropping of *H. ovalis* enhances dry matter digestibility as well as concentrations of organic matter and protein (Aragones 1996), the latter often being a limiting nutrient for herbivores (Mattson 1980).

The ability of *H. ovalis* to increase production of nutrient-rich standing crop in response to regrazing has major implications for seagrass grazers. *H. ovalis* is the preferred seagrass of both green turtles (Read 1991; Brand 1995; Brand-Gardner *et al.* 1999) and dugongs (Preen 1992; Lanyon 2003) in eastern Moreton Bay, possibly because of its relatively high nutrient levels and high digestibility (Lanyon 1991; Brand 1995; Aragones 1996). The grazing pressure on *H. ovalis* in Moreton Bay is likely to be considerable, particularly during the spring–summer months when local densities of grazing herbivores are highest. There are an estimated 10 000 green turtles (C. Limpus, pers. comm.) and some 800 or more dugongs (Lanyon 2003) in an area of 110 km² of seagrasses in eastern Moreton Bay (Preen 1992). There is evidence that large numbers of both green turtles and dugongs regularly regraze areas of the eastern bay that support their preferred seagrasses. Green turtles within Moreton Bay show feeding site fidelity (Read 1991; Limpus *et al.* 1994; Brand 1995), with the same turtles regrazing areas at intervals over periods of 4 months and longer. Herds of grazing dugongs have been observed feeding in the same areas for 3–4-week periods (J. Lanyon, pers. obs.), or returning to regraze particular sites after 4–6 months (Preen 1992, 1995). The present study indicates that by recropping areas in Moreton Bay, green turtles increase the nutritional value of their preferred seagrass, *H. ovalis*. In other parts of the world, the regrazing activities of green turtles (e.g. Bjorndal 1980; Ogden *et al.* 1980) have also been found to enhance certain seagrass species by maintaining plots of young more nutritious growth and altering seagrass morphology and chemistry (Bjorndal 1980; Thayer *et al.* 1984). Furthermore, under regrazing, the intrinsically low growth rates of *H. ovalis* increase to levels that are comparable with morphologically larger seagrasses. It is even probable that sustained grazing may alter community composition in favour of ruderal and grazing-tolerant species such as *H. ovalis*, while standing crops of less-tolerant species are reduced. The ability of *H. ovalis* to maintain biomass of nutrient-rich standing crop in the face of repeated turtle grazing is likely to be advantageous not only for green turtles but for dugongs, where their feeding areas overlap.

The changes that occur to those seagrasses less tolerant to grazing (i.e. *C. serrulata* and *Z. capricorni*) are also potentially relevant to the behaviour and nutrition of grazing vertebrates. Grazing reduced total plant biomass of *Z. capricorni* and *C. serrulata* and caused the width of their leaves to be reduced. Variations in leaf morphology in *Z. capricorni* and *H. ovalis* have been recorded in Moreton Bay previously (Young and Kirkman 1975; Poiner 1984), where smaller leaves were associated with higher tidal elevations and exposure stress. If reduction in leaf width is symptomatic of a stressed plant (Zieman 1975;

McMillan and Phillips 1979; Phillips and Lewis 1983), then regrazing is probably an important stress on *Z. capricorni* and *C. serrulata*. If so, then the change in leaf dimension may be accompanied by other physiological or biochemical changes.

In Moreton Bay and elsewhere in northern and eastern Australia, green turtles show dietary preference for younger blades when feeding on seagrasses other than *H. ovalis* (Bjorndal 1980; Lanyon *et al.* 1989). *Z. capricorni* is the least preferred of the seagrasses ingested by green turtles in Moreton Bay but is a preferred food item in some tropical feeding grounds, e.g. Shoalwater Bay (Brand 1995). In contrast, *C. serrulata* has never been recorded as a primary food source for green turtles in Moreton Bay (Read 1991; Brand 1995), possibly because of its restricted distribution (Preen 1992). Simulated regrazing of these species resulted in a reduced standing crop of thin leaves. Consequently, for green turtles, decreased leaf width may be an important visual cue to seagrass palatability because WSC levels were negatively correlated with leaf width in both *Z. capricorni* and *C. serrulata*. Young grazed *Z. capricorni* leaves also contain higher levels of nitrogen (Aragones 1996), and the narrow-leaf form of *Z. capricorni* is a favoured food item in Shoalwater Bay (Lanyon *et al.* 1989). Interestingly, *Z. capricorni* is usually the least preferred seagrass of dugongs in Moreton Bay and is actively avoided (Preen 1992; A. Preen, pers. comm.). However, dugongs will consume the narrow-leaf form of *Z. capricorni* when it is available, particularly during its fruiting season (Preen 1992), suggesting a higher palatability of the fruit and/or leaves.

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