CHAPTER 6.

FEEDING ECOLOGY

6.1. Introduction

To understand the habitat requirements of dugongs, we need to understand their feeding ecology. At present, that understanding is limited to specific aspects of their feeding and diet. Because dugongs leave conspicuous feeding trails in the seagrass, we know something of their method of feeding (Anderson and Birtles, 1978; Heinsohn et al. 1977; Wake, 1975), although it is still unclear exactly how they harvest and ingest their food (Lanyon, 1991; Marsh, 1989a). The dugong's diet has been relatively well studied (Heinsohn and Birch, 1972; Johnstone and Hudson, 1981; Lipkin, 1975; Marsh et al., 1982). However, since no dietary investigation has been coupled with a study of the seagrass resources, our understanding of dugong food preferences is largely anecdotal.

To date, the ecological role of dugongs in seagrass ecosystems has barely been studied (Anderson, 1986; Anderson and Birtles, 1978; Heinsohn et al., 1977; Wake, 1975). In terrestrial ecosystems, however, the relationships between large mammalian grazers and the grass communities on which they feed are often dynamic and interactive (McNaughton, 1984, 1985, 1989) and grazers can influence the composition and structure of plant communities (McNaughton and Georgiadis, 1986). In this way, large herbivores can impose pattern on the vegetation of whole landscapes (Bakker et al., 1983; Huntly, 1991; McNaughton, 1984). Dugongs are large grazing herbivores that dig up and consume considerable quantities of seagrass (Heinsohn et al., 1977). Hence, in areas where they are common, dugongs may also exert a significant influence on the dynamics of marine plant communities.

The aim of this section, therefore, was to obtain a greater understanding of the feeding ecology of dugongs, particularly in the unstudied area of dugong-seagrass interactions. To this end, I studied the following aspects of dugong feeding:

1. characteristics of feeding sites
2. methods of foraging
3. diet and food preferences and
4. the effects of dugong grazing on seagrass communities.

In Moreton Bay, many of the measurable signs of dugong feeding are ephemeral, being obliterated or disturbed by normal tidal currents or wave action resulting from even moderate winds (due to the pure sand sediment and low seagrass cover). Hence, my collection of data at feeding sites was necessarily opportunistic. Normally, data had to be collected from feeding sites at the time of discovery. The amount of time available at feeding sites varied with the time they were found and weather. SCUBA tank capacity imposed a further constraint. For these reasons, data collection could not be rigidly standardised. The numbers of parameters measured and replicate measurements were largely dictated by the available time.

For clarity, the methods and results sections of this chapter have been grouped by topic. There is a single discussion section.

6.2. Characteristics of feeding sites

Comparison of the biological and physical characteristics of sites where dugongs feed with the distribution of areas with these characteristics, may suggest criteria used by dugongs to select feeding sites.

6.2.1. Methods

Physical and biological characteristics of dugong feeding sites were measured at 29 locations where dugongs had recently fed. With the exception of one inshore site (# 29), all the sites were located in the East study area and most had been grazed by 15 - >200 dugongs (Table 6.1).

It became apparent that the dugongs often fed differently on Z. capricorni than on other species. To clarify these differences, feeding sites containing Z. capricorni were often selected preferentially.

Several parameters were measured within a core area (approximately 20 m diameter) near the centre of each feeding site. Due to time constraints, not all parameters were measured at all sites (Table 6.1).

6.2.1.1. Physical characteristics

Sediments

Sediment characteristics that may have an impact on the feeding efficiency of dugongs were measured at feeding sites for comparison with a series of 'random' sites (used to describe the sediments of the two study areas; see section 2.3). I measured (1) mean grain size, (2) abundance of shells and shell fragments and (3) sediment compaction. Grain size and shell abundance could be relevant to the dugongs' capacity to sieve and masticate the harvested seagrass, while sediment compaction may determine how easily the dugongs can collect the seagrass rhizomes.

The methods of collection and analysis have been described in section 2.3. Only the size of quadrats used to asses shell abundance was different: at 19 feeding sites, 5-11 0.05-m^2quadrats were sampled, while three other sites were sampled with 0.0083-m^2 quadrats ($n = 13$), 0.0083-m^2 quadrats ($n=30$) and 0.0047-m^2 quadrats ($n = 20$) respectively.

Data on grain size and shell abundance were collected at 21 and 22 feeding sites respectively, while sediment compaction was measured at 17 sites.

Depth

To determine the depth of the feeding sites relative to datum, water depth was measured at 27 feeding sites and corrected for tidal height at the time of sampling.

6.2.1.2. Abundance of seagrass and ascidians

The abundance of seagrass was measured at each feeding site. At one site (# 27), the abundance of the colonial ascidian Sycozoa pulchra, on which the dugongs were apparently feeding (see below), was also measured.

Of the 29 sampled feeding sites, three (# 21, 24 and 28) contained at least two distinct seagrass communities, which were each sampled separately (numbered 21-1, 21-2 etcetera).

Initially the abundance of seagrass was estimated as the percentage cover. At each of the first eight feeding sites, two 20 m rope transects were tied to the boat's anchor and positioned so their apex formed a right-angle. Seagrass abundance was assessed in 10 quadrats (0.25 m^2) located at 2 m intervals along each transect (20 quadrats/site). Total cover, and the relative abundance of each species were estimated in each quadrat. If the seagrass in a quadrat had been affected by recent dugong feeding, the quadrat was moved laterally until an intact area was sampled.

To avoid problems of subjectivity associated with the estimates of percentage cover, I subsequently modified the sampling procedure to count the number of shoots of each species of seagrass in haphazardly located quadrats at each site. Quadrats were usually dropped into place as I swam about the site with my eyes closed. If a quadrat fell on an area disturbed by feeding dugongs it was not sampled. The number of quadrats sampled (6-75 per site) was determined by the uniformity of the seagrass meadow, the size of the quadrat and the time available. When seagrass abundance was based on shoot density only, a 0.0225 m^2 quadrat (0.15 m x 0.15 m) was used. When shoot density and/or above- and below-ground biomass were sampled, cylindrical corers with surface areas of 0.0083 and 0.0047 m^2 (0.103 m and 0.078 m diameter respectively) were used. Seagrass abundance determined the choice of corer size (small corer used for dense seagrass). At site 27, the abundance (shoot or stalk density) of seagrass and the stalked colonial ascidian (S. pulchra) was assessed in 23 quadrats (0.149 m diameter) which I dropped at intervals of six fin-strokes as I swam, with closed eyes, along an approximately 50 m transect which traversed the site.

Shoot densities derived from counts of the same samples in the field and in the laboratory are presented (Table 6.2b) because previous work (Chapters 3 and 4) was based on laboratory counts, but in this section shoot densities at some sites were measured by field counts only.

6.2.2. Results

The 29 feeding sites represented the range of feeding sites used by dugongs in the East study area of Moreton Bay. They did not, however, represent a random selection of feeding sites, as sites dominated or co-dominated by Z. capricorni were deliberately over-represented.

6.2.2.1. Physical characteristics

Sediments

There was no significant difference between the mean grain size of sediments at the feeding sites in the East study area and the 'random' sites examined in section 2.3 (one-way ANOVA: df = 1, 27, F = 0.02, p = 0.8864; Figure 6.1).

The sediments at the 'randomly' located sites had a significantly higher shell content than the sediments at the feeding sites (one-way ANOVA: df = 1, 445, F = 16.59, p = 0.0001). This was due in part to the very high shell content at 'random' site W1 (Figure 6.2). Feeding site 28-1 (which was located less than 100 m from 'random' site E4) contained significantly more shell material than any of the other feeding sites and all the 'random' sites except site W1 (Figure 6.2).

The compaction of sediments at the feeding sites was significantly higher than at the 'random' sites (one-way ANOVA: df = 1, 336, F = 12.28, p = 0.0005), however, there was very broad overlap between the two data sets (Figure 6.3). The fact that most feeding occurred in areas with compacted sediments (low penetration), relative to the suite of sediments available (Figure 6.3) may be an artefact of the preference of dugongs to feed in areas of relatively sparse seagrass cover (see below) and the inverse relationship between sediment compaction and seagrass biomass (section 2.3).

Depth

Feeding sites on the seagrass banks of the East study area had an average depth of -0.09 m (SE = 0.08; n = 27) relative to datum. Therefore, at mean high water, the average feeding site was covered with 2.0 m of water (range: approximately 1.5-2.5 m). An unusual site (excluded from the above average) in the Rous Channel was 7 m deep.

6.2.2.2. Abundance of seagrass and ascidians

Six of the seven species of seagrass occurring in Moreton Bay occurred in the sampled feeding sites. I have no evidence that dugongs feed on C. serrulata in Moreton Bay, where it has a restricted distribution (Figure 3.1). Of the 30 sites or sub-sites sampled for seagrass abundance, Halophila species were present in 25, H. uninervis in 14, Z. capricorni in 7 and S. isoetifolium in 2 (Table 6.2a, b & c).

The percentage cover of seagrass at eight of the sites ranged from as low as 1% (SE = 0.1) to a maximum of 27% (SE = 2.9; Table 6.2a).

The total density of seagrass shoots at 13 sites ranged from 319/m^2 (SE = 87) to 8,953/m^2 (SE = 346; Table 6.2b). Field counts were always lower than lab counts from the same samples, and ranged from 56% to 80% of the lab counts (Table 6.3). This discrepancy arises because lab counts included shoots that had not emerged above the sediment, and hence, were not visible in the field. The difference between field and lab counts was less for seagrass in grazed feeding trails (Table 6.3) because the surface sediments had been pushed aside, revealing the young shoots.

Seagrass biomass was measured at 13 sites (Table 6.2c). Above-ground biomass ranged from 1.7 g/m^2 (SE = 0.3) to 208 g/m^2 (SE = 14.3), but more than half the sites (54%) contained less than 20 g/m² (Table 6.2c). Below-ground biomass ranged from 7.9 g/m² (SE = 1.5) to 349 g/m² (SE = 17.9). Almost half of the sites (46%) contained less than 50 g/m² of rhizomes and roots (Table 6.2c).

At site 27 the density of the colonial ascidian, S. pulchra, was 1,077 stalks/m² (SE = 319), compared with a total seagrass density of 252 shoots/m² (Table 6.2b).

6.3. Methods of foraging

Grazing is disturbance (Huntly, 1991), so an understanding of the way in which dugongs graze seagrass is necessary for an understanding the dugongs' relationship with the seagrass. The way in which dugongs forage for seagrass may also be relevant to their selection of feeding sites.

Although I was not able to usefully observe dugongs feeding from underwater, dugongs leave many signs of their foraging, which allow their feeding methods to be deduced. Most commonly, dugongs forage on seagrasses by excavating the plants as they swim forward. In the process, they produce distinctive trails, referred to as feeding trails. I examined the size of feeding trails and the proportion of seagrass (and ascidians) removed from them.

6.3.1. Methods

6.3.1.1. Feeding trail dimensions

The number of feeding trails measured was limited by two constraints. The seagrasses in the East study area grow on sand (Figure 6.1), and the edges of the feeding trails begin to collapse immediately after formation. Hence, it was rarely possible to measure the widths and depths of feeding trails accurately. Furthermore, where the density of feeding trails was high, the ends of individual feeding trials often could not be determined.

The lengths of feeding trails were measured at five locations, and the widths at two locations (Table 6.1). It was never possible to measure the depth of the feeding trails accurately.

6.3.1.2. Proportion of seagrass removed from feeding trails

The proportion of seagrass, and ascidians, removed by feeding dugongs was measured by comparing the abundance of seagrass in feeding trails with the abundance of seagrass immediately adjacent to the trails at 10 feeding sites. At two of these sites (# 24 and # 28), feeding occurred in each of two distinct seagrass communities, and the removal of seagrass was measured in each, making a total of 12 sites.

Seagrasses were sampled in 8-21 circular quadrats (0.103 m diameter) located haphazardly along several feeding trails, and in an equivalent number of matched quadrats positioned immediately adjacent to the feeding trails (0.2-0.5 m away). At site 27 the abundance of the ascidian Sycozoa pulchra was measured in 31 quadrats (0.149 m diameter) located haphazardly along feeding trails and in 31 quadrats immediately adjacent to the feeding trails.

Many seagrass meadows are too heterogeneous to be able to use the occurrence of species in particular quadrats adjacent to feeding trails as a measure of the seagrass that was in matched quadrats in the feeding trail. The seagrass 0.2-0.5 m from the trail may not always be the same as the seagrass that was in the feeding trail. Hence, the amount of seagrass, or ascidians, removed from the feeding trails at each site was determined by subtracting the mean abundance of seagrass along the feeding trails from the mean abundance immediately adjacent to the feeding trails.

Seagrasses have different morphologies and growth patterns, and these differences may influence the way they are harvested by dugongs. To elucidate the pattern of removals, the following parameters were measured in each quadrat: shoot density (laboratory count), above-ground biomass, rhizome biomass and root biomass (in samples from site 18, rhizomes and roots were not separated).

When the assessing the efficiency by which a species of seagrass was removed by dugongs, I analysed data only from sites dominated or co-dominated by that species. I assumed that the dugongs foraged in response to the dominant species and ingested other species incidentally.

6.3.2. Results

6.3.2.1. Feeding trail dimensions

The lengths of 74 feeding trails differed significantly between five sites (one-way ANOVA: df = 4, 69, F = 11.48, p = 0.0000). Least Significant Difference comparisons showed that one site, site 6, differed significantly from the other four. At site 6 the feeding trails averaged 4.79 m (SE = 0.28) compared with 2.27 m (SE = 0.14) at the other sites. The feeding trails at site 6 were also wider than those at site 12, the other site at which this parameter was measured (one-way ANOVA: df = 1, 115, F = 214.53, p = 0.0000). At site 6 (10 measurements from 10 feeding trails) the feeding trails were 22.7 cm wide (SE = 0.6) compared with 11.8 cm (SE = 0.2) at site 12 (107 measurements from 32 feeding trails).

The sediment compaction (Figure 6.3), sediment shell content (Figure 6.2), seagrass abundance (Table 6.2a) or depth of site 6 were unexceptional. Without further data, it is difficult to reconcile the difference between the long, wide feeding trails recorded at site 6 with the smaller trails at the other sites.

There was no correlation between the mean length of feeding trails and the density of seagrass shoots at the four sites (# 12, 13, 14, 17) where data on both parameters were collected (r = -0.0771, n = 4, p = 0.9229). These sites spanned a range of shoot densities from 261-2,950 shoots/m^2 (Table 6.2b). At site 28-2, however, where S. isoetifolium occurred at the exceptional density of 8,732 shoots/m^2 (Table 6.2b), feeding trails were noted to be only 30-50 cm long (field notes: 22-11-89).

At site 12, where I displaced the feeding dugongs, the trails were about 4 cm deep, but they had already started to fill with sand. Both broken and intact rhizomes occurred at a depth of about 6 cm, suggesting that this was the depth to which the dugongs were removing seagrass.

6.3.2.2. Proportion of seagrass removed from feeding trails

The amount of seagrass removed from feeding trails was measured at 12 sites and the amount removed of the ascidian Sycozoa pulchra was measured at an additional site (Table 6.1). H. ovalis was present at nine sites and dominated or co-dominated five. Z. capricorni thin dominated or co-dominated all five sites in which it occurred. H. uninervis was present at five sites, of which one (# 16) was co-dominated by the thin morph, and one (# 28-1) was dominated by the broad-leaf morph. H. spinulosa occurred at two sites, which it co-dominated. S. isoetifolium dominated one of the two sites in which it occurred.

There was a significant difference between the abundance of each seagrass component (shoot density, shoot biomass, rhizome biomass, root biomass) between feeding trails and adjacent areas (Table 6.4). Naturally, there was also a significant difference in the abundance of seagrass at different sites (Table 6.4). Because there were significant interactions between the amount of seagrass in, and adjacent to feeding trails and site (Table 6.4), the data have been plotted (Figure 6.4). It is clear that the amount of seagrass removed along feeding trails varied between sites. The difference between sites was due partly to the nature of the different species, and partly to different methods of grazing used on different species (see below). At some sites, the mean biomass of roots was greater within the feeding trails than in adjacent areas (Figure 6.4), which demonstrates the small-scale patchiness of some seagrass meadows.

Dugongs removed over 90% of both the number of shoots (or stalks of ascidians) and the above-ground biomass of four of the six species of seagrass and ascidian harvested along feeding trails at the sites where each species of seagrass was dominant or co-dominant (Table 6.5). The shoots of H. uninervis and Z. capricorni thin were harvested less effectively (72% and 83% removal, respectively) than the other species (one-way anova: df = 1,13, F = 7.51, p = 0.0169; proportions arcsine transformed). The narrow, strap-like leaves of these two species differ strikingly from the other species, and may account for the different cropping efficiencies.

There was greater variation in the proportion of rhizomes and roots of different species removed along feeding trails. While 97% of the rhizomes and 81% of the roots of H. spinulosa were removed, comparable values for H. uninervis were only 46% and 8% (Table 6.5). These differences may be due to variation in the strength of the roots and rhizomes between the different species. In the case of Z. capricorni, however, the relatively low proportions of rhizomes (36%) and roots (21%) removed by dugongs from feeding trails is due to a different mode of grazing.

Under most circumstances the dugongs created furrows through the seagrass and sediment as they harvested the leaves and excavated the rhizomes. Sometimes, however, they cropped only the leaves, causing minimal disturbance to the rhizomes. Such surface grazing was most commonly seen in areas of dense Z. capricorni. Table 6.6 details the proportion of seagrass removed from feeding trails at five sites dominated or co-dominated by Z. capricorni. At site 22, the thin-leaved Z. capricorni was furrow grazed, and 76% of the rhizomes were removed. At site 18, a high biomass site, leaves were surface grazed: only 5.8% of the below-ground biomass was removed. The apparent absence of rhizome grazing at site 24-2 was an artefact due to the low biomass of Z. capricorni. My field notes indicate that the heavily grazed site was predominantly furrow grazed. At sites 24-1 and 25, both surface and furrow grazing were apparent and, hence, the data in Table 6.6 average over both types of feeding. In the areas where Z. capricorni was surface grazed, the rhizome and root mat was very dense and this may have prevented furrow grazing.

The dugongs surface grazed the erect colonies of S. pulchra which carpeted site 27. The holdfasts of this species are very shallow, so it was not necessary for the dugongs to plough through sediment to harvest them.

Lumping all species at each of the 12 sites, 85.6% (SE = 3.8, n = 12 sites) of shoots were removed along feeding trails, compared with 90.8% (SE = 2.6, n = 12) of above-ground biomass, 58.5% (SE = 8.7, n = 11) of rhizome biomass and 25.1% (SE = 6.9, n = 11) of root biomass. The total biomass was reduced by an average of 53.1% (SE = 7.3) at all sites, or 65.2% (SE = 8.4) if the sites dominated by <u>Z. capricorni</u> are excluded.

The proportion of seagrass removed from feeding trails was not correlated with the mean abundance of seagrass adjacent to the feeding trails at the 12 sites (shoot density: r = -0.3104, n = 12, p = 0.32613; above-ground biomass: r = 0.2867, n = 12, p = 0.36627; rhizome biomass: r = 0.0525, n = 11, p = 0.87127; root biomass: r = 0.1352, n = 11, p = 0.67526).

6.4. Diet and food preferences

Direct observation of feeding dugongs is difficult because they are secretive and often generate clouds of sediment. Less direct approaches are required. Stomach analysis would have provided the best indication of diet, however, only three dugong stomachs became available during the study. In contrast, faecal samples were readily available. However, the study of diet through the analysis of faecal material can be problematic because of differential digestion of different foods. Indirect evidence of feeding can provide a complementary picture of food preferences of dugongs.

I attempted to document the diet and food preferences of the Moreton Bay dugongs by:

1. analysing faecal samples
2. analysing stomach samples
3. recording the species of seagrass where dugongs were encountered
4. comparing the seagrasses eaten from feeding trails with the seagrasses present at the site
5. documenting avoidance of vegetation patches.

6.4.1. Analysis of faecal samples

6.4.1.1. Methods

Faecal samples were collected from the sediment or seagrass of the banks and channels of the East study area and frozen for storage. To minimise biases due to year, season or location of collection, a stratified random sub-sample of 48 faecal samples was processed for dietary analysis.

Preparation of the reference collection for seagrass and algae identification

I used fresh or fixed material to assemble a reference slide collection that illustrated the characteristic epidermal features of the seven species of seagrass and seven of the species of algae that occur in Moreton Bay. For each species of seagrass, sections of leaf blade, petiole, sheath, rhizome and root were scraped or peeled with a scalpel and needles under a dissecting microscope to remove mesophyll. The leaf blades of macro-algae were similarly treated. The remaining tissue was soaked in commercial bleach (5% sodium hypochlorite) for 5 to 15 minutes and more of the mesophyll was removed with a scalpel or brush. The cleaned epidermis was rinsed in fresh water and mounted in glycerine jelly on a microscope slide.

Epidermal features were photographed under Nomarski interference contrast lighting at magnifications of 12.5X, 31.25X and 62.6X. A catalogue of prints was assembled (final magnifications = 62, 156 and 313 times) and a table of the characteristics of the epidermal cells from each region (root, rhizome, sheath, leaf) of each species of seagrass and alga was compiled.

Preparation of faecal samples

Figure 6.5 details the protocol for sample preparation. Material that passed through the 4 mm and 500 μm sieves was made up of bacteria, diatoms, mucus, sloughed cells and very small fragments of plant material, and was not retained.

On average 40% (SE = 1.8) of the wet-weight of each faecal sample was retained by the sieves. Subsequent references to the abundance of components refer to their abundance in the retained material.

Microscopic examination of material retained by the 500 μm sieve

A sub-sample of the material retained by the 500 μm sieve was cleared and a small amount spread evenly over microscope slides (63 mm x 24 mm), to obtain thorough and complete coverage with minimal overlap of material. Several drops of alcohol (70%) were added and a coverslip applied.

The abundance of each category of material was determined by two methods:

Method 1: Three slides were prepared from each sample. Each slide was thoroughly searched at 40X magnification to identify all material present. At each of five pre-determined locations per slide, material was identified at 42 points, located by the etched lines of a Weibel graticule eye piece.

Method 2: Two slides per sample were systematically and completely searched at 40X magnification, and the relative abundance of all identifiable material was visually estimated relative to the total amount of material on the slide. This relative scale ensured that the estimate was independent of the density of material, which varied between slides.

Twenty-one faecal samples were examined using both methods. There was no significant difference between the estimates of abundance resulting from the two methods (Table 6.7). Due to the low proportion of identifiable seagrass (mean = 12.3%; SE = 4.4%), Method 1 was time consuming and inefficient, so subsequent samples were analysed using Method 2.

Composition of faecal samples

Method 2 estimates the relative surface area of each category of the material. This, in turn, is approximately equal to relative volume (Galt et al., 1982).

Assuming similar specific densities for all material in the samples, volume will approximate wet weight.

The abundance of each category of material in each sample, expressed as a percentage of the wet weight of that sample, was determined by:

$$\frac{(a.x)+(b.y)}{(x+y)}.100$$

where:

a = mean surface area (%) of the specific category of material on the two microscope slides of material retained by the 500 μm sieve

b = percentage wet weight of material retained by the 4 mm sieve that was composed of the specific category

x = wet weight of material retained by the 500 μm screen

y = wet weight of material retained by the 4 mm screen

Only seagrass leaf material could be identified to species or genus. Rhizome, root, sheath and cuticle material (collectively referred to as rhizome) could not be identified due to extensive overlap of the shapes and dimensions of epidermal cells between species and genera. H. ovalis and H. spinulosa could be separated only if the leaf fragment included part of the leaf edge.

Temporal patterns in faecal composition

Seasonal and inter-year variation in the relative abundance of the four most common categories of identifiable material was examined by analyses of variance. Three seasons (winter, spring, summer; see section 2.2 for definitions; insufficient samples were collected in autumn) and two years (1988-9 and 1989-90) were considered. Untransformed data were used, as the plotted residuals did not indicate that arcsin transformations improved the fit of the models. The effect of collection location was not examined, as it may be an unreliable index of feeding location due to the dugong's long gut passage rate (6-7 days; Lanyon, 1991). Approximately equal numbers of samples were analysed from each of three main collection areas (northern, southern and central sections of the East study area) within each season by year combination, so the overall result is unlikely to be confounded with collection area.

6.4.1.2. Results

Seagrass

Unidentifiable rhizome occurred in all faecal samples, comprising an average of 62% of their wet weight (Table 6.8).

Leaf material from five species of seagrasses was identified in the faecal samples. Z. capricorni was the most abundant, occurring in 88% of samples and making up 11% of their wet weight (Table 6.8). Halophila species (H. ovalis and H. spinulosa) occurred in 79% of samples, but constituted only 3% of their bulk. H. uninervis and S. isoetifolium were present in 23% and 6% of samples respectively, but contributed insignificantly to their volume (Table 6.8).

There were no significant effects of year or season on the abundance of Z. capricorni or Halophila species in the faecal samples (Table 6.9), although there were significant year by season interactions for both taxa (Table 6.9). However, plotting of cell means indicated that there was no predictable seasonal pattern in the abundance of Z. capricorni or Halophila species in the faecal samples.

Ascidians

The stalks of the colonial ascidian S. pulchra were the second most abundant item in the faecal samples. S. pulchra occurred in 69% of samples, making up an average of 29% of their bulk (Table 6.8). S. pulchra stalks comprised more than half of the wet weight of 18% of samples. There was a significant influence of season on the abundance of S. pulchra in the faecal samples (Table 6.9). Although the ascidians were present during each season, Least Significant Difference comparisons established that the abundance of S. pulchra in spring was significantly greater than in winter or summer.

The mantles of solitary ascidians (including Polycarpa obscura, P. pigmentata and P. fungiformis) were also conspicuous in the faeces, occurring in 27% of samples, and making up an average of 20% of their bulk (Table 6.8). Most faecal samples containing solitary ascidians contained only one or two mantles (mean = 3.9, SE = 1.96) but one sample contained 28. Neither year nor season had a significant effect on the abundance of solitary ascidians in the faeces (Table 6.9).

Algae

Algae were found in only three samples (6.3%; Table 6.8). They were present in insignificant quantities (<0.5%) in two samples, but constituted 20% of the bulk of the third.

'Other' items

'Other' material identified in the faecal samples (Table 6.8) included non-parasitic macro-invertebrates (worms, worm tubes, shells, colonial hydrozoans, and unidentified animal material), seagrass seeds and tree bark. One or more of these items occurred in 44% of samples, but they comprised only 2% of their wet weight. 'Other' invertebrates (cf. 'other' material) occurred in 33% of samples, making up 2% (SE = 0.78%) of their wet weight.

6.4.2. Analysis of stomach samples

6.4.2.1. Methods

Only three stomach samples were collected from dugong carcasses during the study. These were stored in formalin before being processed in the same manner as the faecal samples (Figure 6.5, and above).

6.4.2.2. Results

The three stomach samples differed in species content and in the relative proportions of leaf and rhizome material (Table 6.10). The contents of stomach MB-1 comprised three discrete zones, suggestive of at least three feeding sessions. One zone was composed almost entirely of Z. capricorni (20% rhizome, 80% leaves); the second a mixture of H. ovalis and Z. capricorni; and the third consisted entirely of a colonial polychaete (family Chaetopteridae) and its tubes. The stomach of dugong MB-2 consisted almost entirely of Z. capricorni leaf. MB-2 was killed on an inshore (western Bay) seagrass bed dominated by thin-leafed Z. capricorni. The stomach of dugong MB-3 mainly contained H. ovalis, but also had some Z. capricorni, H. uninervis, S. isoetifolium and an alga.

6.4.3. Incidence of invertebrates in the diets of tropical dugongs

Invertebrates have not previously been recorded as a significant component of the diet of dugongs. However, most analyses have been done on stomach (Gohar, 1957; Heinsohn and Birch, 1972; Lipkin, 1975; Marsh et al., 1982; Spain and Heinsohn, 1973) or mouth (Johnstone and Hudson, 1981) contents. In order to determine whether results from Moreton Bay were due to geographic rather than methodological differences, I examined the incidence of macro-invertebrates in the diets of dugongs from tropical areas.

6.4.3.1. Methods

Thirty-three stomach samples and 15 rectal samples were examined from 48 dugongs from north Queensland (Townsville: 19°25'S, 146°15'E; Hopevale: 14°45'S, 145°18'E; and the Wellesley Islands: 16°30'S, 139°30'E) and Papua New Guinea (Daru: 9°5'S, 143°12'E). The formalin-fixed samples came from the collection of the Zoology Department, James Cook University. Details of collection procedures are recorded in Marsh et al. (1982). The samples were prepared following the protocol set out in Figure 6.5 and detailed above.

The seagrasses in the samples were not identified or quantified for two reasons. Firstly, complementary data on the availability of seagrasses is not available for the samples. Secondly, Heinsohn and Birch (1972) and Marsh et al. (1982) have examined the diet of dugongs using samples form the same collection from which

I drew my sub-sample. It should be noted, however, that the collection has grown and the origin of new samples has changed over time.

6.4.3.2. Results

Thirty seven percent of stomach and rectal samples from north Queensland and Papua New Guinea contained material other than seagrass. There was no significant difference in the occurrence (X^2 with Yates correction = 1.4848, df = 1, $p > 0.1$) nor the abundance (t-Test with unequal variance: t = -1.79, df = 32, p = 0.0831) of invertebrates in the rectal and stomach samples. Invertebrate material was present in 29% of samples, making up 1.2% (SE = 0.6) of their wet weight (Table 6.11). This abundance is inflated by six small holothurians (7.8% of wet weight) in one stomach sample. Most items occurred infrequently in the samples, at a low rate of abundance. Ascidians occurred in 6.2% of samples, but constituted only 0.04% of the bulk of all samples. Equivalent values from the Moreton Bay samples were 72.9% and 25.5%.

6.4.4. Species of seagrass present where dugongs were encountered

The pattern of dugong distribution revealed by the aerial surveys and satellite tracking, integrated with data on seagrass distribution, has provided a broad picture of the dugongs' feeding areas in Moreton Bay. However, the combined errors of these techniques means that the spatial resolution of these results is measured in hundreds of metres (see sections 3.2.6.2 and 5.2.1.3). To obtain a higher resolution of dietary selection, I recorded the species of seagrass present wherever I encountered groups of dugongs on the seagrass banks. This approach assumes that the dugongs I encountered were feeding, an assumption supported by observation.

6.4.4.1. Methods

Whenever I encountered groups of dugongs on the seagrass banks, I recorded the seagrass species present as well as a qualitative estimate of seagrass abundance (sparse, medium, dense). These data were usually recorded from areas 5-50 m in diameter, depending on the size of the dugong group.

These data were collected either:
1. opportunistically, when dugongs were encountered during routine activities or
2. during deliberate searches for dugongs.

As I tended to search areas where dugongs were most likely to be encountered, the data from the second category are biased. To minimise the effect of this bias I consider only the number of groups associated with each seagrass, not the number of dugongs (largest herds occurred in the searched areas).

6.4.4.2. Results

I recorded the species and abundance of seagrass where 115 herds (containing an estimated 4,000 dugongs) were encountered (Table 6.12). Species of Halophila occurred at 99% of the sites where dugongs were encountered. H. ovalis was present at 89% of the sites, H. spinulosa at 63% and H. decipiens at 3%. Halodule uninervis was found at 19% of locations where dugongs were found. Z. capricorni occurred at 13% of sites. Only 1 site contained S. isoetifolium and no sites contained C. serrulata.

6.4.5. Selective feeding within seagrass communities

For evidence of selective grazing I compared the species composition of seagrasses and ascidians along feeding trails with their availability at the feeding sites generally.

6.4.5.1. Methods

At each of seven feeding sites a weighted line was laid along the lip of well-defined feeding trails and the species of seagrass nearest to the line was recorded at marked intervals of 5 cm. Data from an average of 162 (range = 57-580, SE = 65.5) points were recorded at each site (Table 6.13). Assuming that these data represented the species that had been removed along the feeding trails, I calculated the relative frequency of grazed seagrasses.

The relative frequency of each species of seagrass at the feeding site (cf. along the edges of the feeding trails) was measured by estimating percentage cover or by counting shoot densities in quadrats located along transects or placed haphazardly (section 6.2.1.2; Table 6.2a and b). Selection or avoidance of seagrass species was indicated by the difference between a species' relative frequency at the site in general and along the edge of feeding trails.

The expected frequency of each species at the site generally, was calculated by multiplying its relative frequency (above) by the number of points recorded along the edge of the feeding trails at that site. These frequencies were then compared with the frequency of species along the feeding trails using Chi-square Goodness of Fit tests.

The density of colonies of S. pulchra in 31 quadrats (0.149 m diameter) adjacent to feeding trails were compared by analysis of variance with their density at the site generally. The density of colonies at the site was determined by counting colonies in 23 quadrats placed at intervals of six fin-strokes as I swam, with closed eyes, for approximately 50 m across the site. This approach was legitimate due to the high abundance and relative uniformity of the ascidian, S. pulchra, at site 27.

6.4.5.2. Results

Seagrasses

At two of seven sites, the frequency of seagrasses along the edges of feeding trails differed significantly from the expected frequency (based on the abundance of species at the sites; Table 6.13).

At one of these sites (# 2) Z. capricorni broad was scattered throughout the meadow, as well as occurring in mono-specific patches. The frequency of seagrasses along the feeding trails indicates that the dugongs had a clear preference for areas where H. spinulosa was most abundant, and that they avoided areas dominated by Z. capricorni. H. ovalis was neither selected for, nor avoided (Table 6.13).

At the other site (# 17), the dugongs avoided areas dominated by either H. spinulosa or Z. capricorni and selected areas dominated by H. ovalis. At this site, the seagrass occurred in three zones: an area dominated by dense H. spinulosa, an area dominated by dense Z. capricorni and a polyspecific area dominated by H. ovalis but including Z. capricorni, H. spinulosa and some H. uninervis. No feeding trails were located in the dense patches of Z. capricorni or H. spinulosa (which was supporting a heavy growth of epiphytic algae; see below).

At the two sites containing Z. capricorni, the distribution of seagrasses along the feeding trails indicated avoidance of this species. By comparison, H. ovalis occurred at all seven sites and was selected for at one and avoided at none. H. spinulosa occurred in six sites and was selected for at one and avoided at one (where it was covered with epiphytic algae). H. uninervis was found in 2 sites and was consumed in proportion to its abundance at both (Table 6.13).

Ascidians

At site 27, the abundance of S. pulchra colonies was significantly greater in the quadrats adjacent to the feeding trails (3,618 colonies/m^2, SE = 664) than at the site generally (1,077 colonies/m^2, SE = 319; one-way ANOVA: df = 1,52, F = 9.28, p = 0.0036; Table 6.13), suggesting that the dugongs selected patches with high abundance of S. pulchra. The dugongs were not selecting seagrass at this sparsely vegetated site. The cover of seagrass (H. decipiens, H. spinulosa and H. ovalis) was sparser adjacent to the feeding trails (75 shoots/m^2; SE = 31) then at the site generally (252 shoots/m^2; Table 6.2b).

6.4.6. Avoidance of patches of Z. capricorni broad

Evidence of selective grazing was also obtained by comparing grazing pressure in different seagrass patches within feeding sites.

6.4.6.1. Methods

Three feeding sites (# 2, 14, 24) included dense patches of Z. capricorni that appeared to be avoided by grazing dugongs. This avoidance was quantified by measuring the density of feeding trails in these patches and in the surrounding seagrass community. I dragged a 5 m-long weighted rope through each area as I swam haphazardly with my eyes closed and periodically measured the length of sections of the rope-transect that overlaid feeding trails. Eight to forty transects were measured in each area.

At a fourth site (# 21), where I could walk about at low tide, I counted the total number of feeding trails in adjoining, mono-specific patches of Z. capricorni, S. isoetifolium and H. uninervis, rather than estimating the proportion of the area occupied by feeding trails.

At a fifth site (feeding site # 28), the grazing pressure in the seagrass community surrounding the ungrazed patches of Z. capricorni was so great that it was not possible to measure the density of feeding trails. Instead, I attempted to determine the level of Z. capricorni abundance that deterred the grazing dugongs. Three cores (0.078 m diameter) of seagrass and sediment were taken at 20 cm intervals along transects which ran perpendicular to the interface between the ungrazed Z. capricorni and the grazed H. uninervis to measure the amount of Z. capricorni rhizome in the grazed areas. Cores were taken from five transects located around the perimeter of each of two patches of Z. capricorni (10 transects). The patches were approximately 10 m diameter.

6.4.6.2. Results

Feeding trails occupied only 1.7%, 0% and 1.1% of the areas of dense patches of Z. capricorni at sites 2, 14 and 24 respectively. Comparable densities of feeding trails in the surrounding seagrass communities at these sites were 28.8%, 6.6% and 16.5% (Table 6.14).

Similar selective grazing was noted at site 21. Of 127 feeding trails, 88.2% occurred in the area of pure H. uninervis (site 21-1; Tables 6.2b and c) and 11.8% in the area of S. isoetifolium (site 21-2; Tables 6.2b and c). No feeding trails were found on the area of Z. capricorni broad.

At site 28, the dugongs grazed right to the edge of the Z. capricorni patches (in fact some feeding trails followed the patch edge), but they did not transgress the boundary of Z. capricorni. No rhizomes or roots of Z. capricorni were found in 10 core samples taken approximately 10 cm beyond the patches' boundaries, where most of the H. uninervis had been removed by grazing (Table 6.15). Just 10 cm inside the Z. capricorni patches, H. uninervis made up 46% of the total seagrass biomass, but the dugongs did not graze this (Table 6.15).

6.4.7. Feeding on Z. capricorni seeds

Although I was unable to find any significant grazing of areas of high biomass Z. capricorni broad, dugongs did not avoid all Z. capricorni dominated communities. Dugongs grazed Z. capricorni thin at at least four inter-tidal locations (Table 6.16). At at least three of these sites, the Z. capricorni thin was fruiting at the time they were grazed, suggesting that dugongs may have fed in the areas because of the fruit. Some Z. capricorni seeds were found in dugong faeces (Table 6.8).

6.4.7.1. Methods

The number of reproductive shoots was recorded when shoots from samples were sorted and counted in the lab.

6.4.7.2. Results

The Z. capricorni thin at sites 18, 24-1, 24-2 and 25 was fruiting at the time these sites were grazed (Table 6.16). Although no data were collected on the reproductive state of Z. capricorni at site 22, the date that it was grazed, relative to the other sites, suggests that it may have been fruiting also (Table 6.16).

At sites 24-1 and 25 there were 1,036 and 1,021 reproductive shoots of Z. capricorni thin/m^2 (Table 6.16). Each reproductive shoot contained 1-4 spathes which contained up to 10 ovoid seeds (2 mm by 1 mm). Assuming an average of two spathes containing 5 seeds per reproductive shoot, these beds contained >10,000 seeds/m^2. At a weight of 0.75 mg/seed (Wassenberg, 1990) with 60% digestible carbohydrate (Dall et al., in press), these seeds represented about 4.5 g digestible carbohydrate/m^2. In comparison, the leaves alone would have contained an estimated 2.7 g soluble carbohydrate/m^2 (3.52% soluble carbohydrate [Lanyon, 1991] and 76 g/m^2 above-ground biomass [Table 6.6]).

Only 1.7% of shoots of Z. capricorni thin at site 24-2 were reproductive. This site, which had a sparse cover of Z. capricorni, adjoined site 24-1, which supported a high abundance of Z. capricorni (Tables 6.6, 6.2b and c). Site 24-2 was extensively grazed at the time of sampling. It is possible that the quadrats used to sample the seagrass at this site sampled regrown shoots, thus accounting for the low incidence of reproductive shoots.

In no area was Z. capricorni broad found to contain a density of seed comparable the above areas of Z. capricorni thin. Due to pollination requirements, Z. capricorni has a much greater fecundity when growing in inter-tidal areas (thin-leaf morph in the East study area) than sub-tidal areas (broad-leaf morph; I. Poiner, pers. comm.).

6.5. The effects of dugong grazing on seagrass communities

In Moreton Bay, dugongs frequently feed in large herds (Chapter 7), often at the same location for extended periods (Table 5.4). The size of the herds and the duration of grazing determine the areal extent and degree of seagrass disturbance caused by the dugongs. In this section, I examine the ecological effects of dugong grazing on seagrass communities. To this end I:

(1) monitored the grazing and recovery of heavily-grazed areas, and

(2) conducted a series of manipulative experiments to simulate dugong grazing in a mixed seagrass community.

6.5.1. The grazing and recovery of feeding areas

6.5.1.1. Methods

The abundance of seagrass prior to, and following, intensive grazing by dugongs was measured at three areas, and the recovery of two of these areas was monitored.

Area 1

The abundance of seagrasses was measured by counting the number of seagrass shoots in 18 haphazardly located quadrats (0.0083 m^2) the day grazing commenced (9-1-90) at the site (feeding site # 26). Sampling was restricted to the region (approximately 20 m diameter) around the initial feeding trails. This area contained the seagrasses H. ovalis, H. spinulosa, H. uninervis and Z. capricorni (Table 6.2). The area was resampled after 12 days of intensive grazing. Seagrass shoots were counted in 110 quadrats (0.0047 m^2) haphazardly located over an area of approximately 2 ha.

Area 2

Between 17-8-89 and 29-11-89 as many as 219 dugongs grazed a large area (approximately 2.5 km by 0.3 km) of seagrass on the western edge of the Coonungai Bank. In the area sampled, patches of Z. capricorni broad (1-20 m diameter) were scattered through a matrix of H. uninervis broad. Patches of S. isoetifolium were located mainly along the eastern boundary. Feeding site 28 occurred within Area 2.

The area was not sampled until after it had been extensively grazed (22-11-89). 'Pre-grazing' seagrass abundance in the H. uninervis zone was determined from 10 quadrats (0.0047 m^2) located in ungrazed clumps of seagrass located adjacent to feeding trails.

Recovery of the seagrass was monitored over 5 months after grazing had finished.

Three permanent north-south oriented transects (H1-H3) were established in the H. uninervis zone on 22-11-89. Each transect was 20 m long with quadrat markers located at 2 m intervals. Transect H1 was located 210 m north of transect H2, which was 200 m north of H3. The seagrass was sampled in 10 quadrats (0.05 m^2) from each transect on 22-11-89, 21-1-90 and 1-5-90. The precautions described in section 4.2.1 were followed to ensure that quadrats sampled different locations along the transects in each sampling period.

Area 3

Between 6-3-89 and 23-3-89 as many as 459 dugongs fed on a luxuriant patch of H. ovalis at AO's Bank (Case 1, Table 5.4). Pre-grazing abundance of seagrass was assessed on 8-3-89 in 17 quadrats (0.0225 m^2) haphazardly located around some recent feeding trails (Figure 6.6a, b). This was feeding site 12.

The recovery of the seagrass community was monitored for over 9 months. Three transects (G1-G3; equivalent to those at Area 2) were established on 23-3-89, after the area had been extensively grazed. The transects were located approximately 150 m apart and together they sampled a 16 ha tract of seagrass within a 41 ha grazed area. Ten quadrats (0.05 m^2) were sampled along each transect (as described for Area 2) on six occasions between 23-3-89 and 7-1-90.

Area 3 was intensively grazed twice during the period of monitoring, once at the beginning (referred to as 3-1) and again 6 months later (3-2). Therefore, the proportion of seagrass removed by dugongs was measured on four occasions at three areas (Table 6.17).

To provide an indication of the recovery, relative to the expected abundance of seagrass in the absence of grazing, the pre-grazing levels of seagrass abundance at Areas 2 and 3 were adjusted for seasonal growth patterns and plotted for each sampling period (Figures 6.7 and 6.8). Species-specific correction factors for each season for above- and below-ground parts were derived from data in Chapter 4. Pre-grazing estimates of shoot density and biomass were available from Area 2, while shoot density only was available for Area 3 .

6.5.1.2. Results

The affects of dugong grazing are illustrated in Figure 6.6, which shows the results of a few hours (<4 hours) grazing by about 70 dugongs at a location in Area 3.

Amount of seagrass removed

At Area 2, shoot density, above-ground biomass and below-ground biomass was reduced by 65%, 73% and 31% respectively (Figure 6.7; Table 6.17). Grazing was more intensive at Areas 1, 3-1 and 3-2, where the number of seagrass shoots was reduced by 87%, 95% and 92% respectively (Figure 6.8; Table 6.17). At Area 3-2 the biomass of seagrass was reduced by 96% and 71% for the above- and below-ground components respectively (Table 6.17).

These reductions represent the removal of large amounts of seagrass because large areas were affected: Area 1: 2 ha; Area 2: 75 ha; Area 3: 41 ha (measured from aerial photographs). At Area 3, I estimate the dugongs consumed over 151,000 kg wet weight of seagrass in under 17 days (Appendix 7.1.2).

Immediately following the second grazing incident at Area 3, the above-ground biomass had been reduced to 0.95 g/m^2 (SE = 0.19) and the below-ground biomass to 8.00 g/m^2 (SE = 1.10): respective reductions of 95.8% and 71.3% of the seagrass abundance prior to the second grazing (Table 6.17; Figure 6.8). Despite the greatly diminished biomass of seagrass, dugongs continued to graze the area at a low intensity. During 6 aerial surveys between 2-10-89 and 2-1-90, an average of 11.5 dugongs (SE = 3.3) were seen on the area. By 23-11-89, when the seagrasses were next sampled, this continued, low-intensity grazing had reduced the biomass of rhizomes and roots to 1.03 g/m^2 (SE = 0.19; Figure 6.8). Compared with the level prior to the second grazing, this was a net reduction of 96.3%. The low-intensity grazing had little impact on the density or biomass of shoots (reducing above-ground biomass to 0.56 g/m^2, SE = 0.11 and reducing shoot density from 118.26 shoots/m^2, SE = 22.02 to 112.41 shoots/m^2, SE = 23.32; Figure 6.8). This may be the minimum level of abundance to which the dugongs can reduce a meadow of H. ovalis. Below a shoot density of about 110-120 shoots/m^2, the dugongs may not be able to harvest the seagrass faster than it can grow (at least during spring and summer).

Recovery

At Area 2, the shoot density and above-ground biomass of H. uninervis recovered to seasonally-adjusted pre-grazing levels within 160 days, which spanned the summer and autumn growing season (Figure 6.7). In fact, the grazing may have stimulated an increase in the abundance of shoots above the level that would have been achieved in the absence of grazing (Figure 6.7). The below-ground biomass, however, was much slower to recover, largely because it continued to decline after the grazing had finished (Figure 6.7). This response may have resulted from the eventual death of some small sections of rhizome created by the high density of crisscrossing feeding trails.

At Area 3, the initial recovery of the seagrass was rapid, despite the severity of the grazing (Figure 6.8). Approximately 150 days after its initial grazing, the average density of H. ovalis had increased from a post-grazing density of 155.9 to 1,445.7 shoots/m^2. In the absence of grazing, the seasonally adjusted shoot density was predicted to have been 2,214.7 shoots/m^2 (Figure 6.8). So, H. ovalis had recovered to more than half (65%) of its seasonally-adjusted, pre-grazing abundance. This recovery had been achieved during autumn and winter, when the growth rate of H. ovalis is at its lowest (section 4.3.2; Figure 4.1).

The second grazing event at Area 3 (3-2) removed 92% of the shoots of the recovering H. ovalis meadow (Table 6.17). Despite a favourable growing period (spring-summer), continued low level grazing by dugongs (see above) was enough to prevent any recovery within the next 100 days (Figure 6.8).

6.5.2. Exclosure experiments

Exclosure experiments were designed to determine the effects of grazing by dugongs on the relative abundance of seagrasses in a mixed seagrass meadow on the Maroom Bank. I attempted to test the following hypotheses:

(1) that low-intensity grazing by dugongs does not change the relative abundance of species in the seagrass meadow

(2) that intense grazing by dugongs does not retard the expansion of Z. capricorni or encourage the dominance of H. ovalis

(3) that the expansion of Z. capricorni on the Maroom Bank is not restricted by a physiological limitation.

These hypotheses were tested by manipulations of the seagrass to simulate dugong grazing, and by using exclosures to protect the treatments from the confounding influences of uncontrolled grazing by dugongs.

6.5.2.1. Methods

Sites

Each treatment was established at each of three replicate sites. A fourth site was used to examine the effect of the exclosures on seagrass growth and survival. Sites were selected that contained approximately equal proportions of Z. capricorni, H. spinulosa and H. ovalis. This mix was chosen as it was similar to feeding site 2, where Z. capricorni was grazed when interspersed with H. spinulosa and H. ovalis.

To minimise the possible loss of data resulting from dugong grazing, the four sites were dispersed over an area of approximately 12 km^2. All the sites were sub-tidal.

Treatments

The three treatments were:

(1) No-grazing: To monitor changes in the abundance of each species of seagrass in the absence of grazing by dugongs. The seagrass was not disturbed.

(2) Low-intensity grazing: Three feeding trails were simulated. The

parallel 'feeding trails' were 1 m apart, 3 m long, 18 cm wide and approximately 6 cm deep.

(3) High-intensity grazing: Intensive grazing was simulated by removing seagrass (shoots and rhizomes) over a 9 m^2 area until the site resembled a heavily grazed meadow (90-95% seagrass removal; see above).

Figure 6.9 shows the schematic arrangement of treatments at one of the three sites.

The effect of the exclosures on the seagrasses was examined at a fourth site by monitoring the seagrasses within an exclosure and within an equivalent unprotected plot (no exclosure) about 2 m away.

Exclosure design

The exclosures were designed to deter dugong and turtle grazing without affecting light and water-flow regimes. The exclosures (Figure 6.9) consisted of wooden stakes projecting 25 cm above the sediment and linked by light (4 mm) rope around the perimeter and across the top. Hence, they formed a 25 cm high fence around the enclosed area with an open net (1 m^2 mesh) over the top. The exclosures would not stop a determined dugong from feeding through the top mesh, but it was hoped that the fence would interrupt the dugongs feeding motion and so prevent feeding trails from crossing the experimental areas. The exclosures were impediments rather than barriers to grazing. The use of the area by boats precluded the construction of higher fences that could have excluded herbivores. The unprotected site was marked with four corner pegs which projected 1 cm above the sediment.

To minimise the influence of very small-scale patchiness in the seagrasses, the abundance of seagrass was monitored over an area of 4 m^2 within each exclosure. To avoid any edge effect, this core area was surrounded by a 0.5 m wide buffer, so the exclosures covered 9 m^2 (3 m x 3 m). The ropes of the exclosures were cleaned of epiphytic algae at intervals of 1-4 weeks.

Monitoring

Shoot density was counted in 0.0225 m^2 quadrats (15 cm x 15 cm) systematically located in each exclosure. Thirty quadrats (six quadrats along each of five transects) were monitored within each exclosure (and the unprotected plot) except in the low-intensity grazing treatment. In that treatment, 18 quadrats were monitored: six quadrats along each of the three simulated feeding trails. A pilot study indicated that at least 14 quadrats would be required to detect a 50% change in abundance. The position of each quadrat was rigidly controlled so repeat counts censused the same locations (±2-5 cm).

The abundance of seagrasses in the low- and high-intensity treatments was measured immediately prior to the seagrass manipulations. The abundance of seagrasses at all sites was then monitored on four occasions (approximately 100 days apart) between late June 1989 and early May 1990.

6.5.2.2. Results

Effect of exclosures

The lack of site replication prevented a statistical comparison between the abundance of seagrass species in the unprotected and exclosure plots at the fourth site. However, it seems apparent from the graphs of the abundance of each species (Figure 6.10) that the exclosure had no pronounced effect on Z. capricorni or H. spinulosa. The abundance of these species in the enclosed and the unprotected plots followed the same pattern over the 10 months they were monitored (Figure 6.10). The exclosure may have had a negative effect on the growth of H. ovalis. This species displayed a summer peak in abundance in the unprotected plot, but not in the adjacent exclosure (Figure 6.10). This response may have been due to shading by the taller Z. capricorni and H. spinulosa, compounded by shading by the epiphytic algae which proliferated, despite regular cleaning of the exclosure ropes. Shading by taller species can be important in the succession of seagrasses (Williams, 1987).

Effects of treatments

The effects of the three treatments (no-, low- and high-intensity grazing) was examined by analysis of variance. The response variable was the log-transformed shoot density ($\log_{10}$(shoot density+1)). Site (random factor) was crossed with treatment (fixed factor). Quadrat (random) was nested within transect (random), which was nested within site*treatment. This combination was all crossed with species (fixed) and time (fixed). The error terms used to test effects are listed in Table 6.18.

As expected, there were significant effects of treatment, time and treatment*time (Table 6.18). The result of interest is the significant interaction between treatment*species*time. To interpret this result, the means of each treatment*species*time combination have been plotted, along with the critical values for Least Significant Difference comparisons (Figure 6.11). Pre-treatment shoot densities (for low- and high- intensity grazing treatments) have also been plotted, although these were not included in the analysis.

(1) No-grazing treatment

In the absence of any grazing disturbance, the abundance of Z. capricorni increased over the 10 month monitoring period, while H. ovalis decreased (Figure 6.11a). Z. capricorni was significantly less abundant than H. ovalis at the start of the experiment, but significantly more abundant at the end. The abundance of H. spinulosa showed no trend comparable to H. ovalis. These results indicate that Z. capricorni was not restricted physiologically at the experimental sites. The data also suggest that H. ovalis may eventually be competitively excluded from this seagrass community.

(2) Low-intensity grazing

Averaged across species and sites, 89% of shoots were removed along the simulated feeding trails (Table 6.19). This reduction is in accord with the level of shoot removal from real feeding trails (72-99%; Table 6.5).

The seagrasses recolonised the 'feeding trails' primarily through ingrowth from the edges. The first 100 days of the experiment corresponded with winter and spring. Consequently, Z. capricorni, which has a winter-spring growth period (Figure 4.1), colonised the 'feeding trails' first. H. ovalis and H. spinulosa have a summer-autumn growth period (Figure 4.1) and were slower to respond (Figure 6.11b). By the end of the experiment, Z. capricorni and H. spinulosa had recovered to pre-treatment levels. H. ovalis, however, was significantly less abundant (Figure 6.11b). These results suggest that within the seagrass community tested, disturbance from low-intensity grazing by dugongs does not alter the relative abundance of Z. capricorni and H. spinulosa, and may even reduce the relative abundance of H. ovalis.

(3) High-intensity grazing

On average, 83% of seagrass shoots were removed from the plots designed to simulate intensive grazing by dugongs (Table 6.19). This compares with reductions of 87%, 65%, 95% and 92% at four heavily grazed areas (Table 6.17).

Recovery of the seagrass within this treatment resulted from the expansion of surviving plants and possibly by seed germination. The winter-spring period at the start of the experiment retarded any recovery for the first 100 days (in contrast with the low-intensity grazing treatments, the Z. capricorni plants were small and would have had few rhizomatous reserves). H. ovalis showed significantly greater recovery than Z. capricorni or H. spinulosa, increasing its relative and absolute abundance during the 100-200 day period (Figure 6.11c). H. ovalis maintained its relative, and significantly greater, abundance during the 200-300 day period (Figure 6.11c).

This experiment supports the hypothesis that disturbance, such as that caused by the extended grazing of a large herd of dugongs, is capable of altering the mix of species in a seagrass meadow for a period of at least 10 months. Fast growing species such as H. ovalis are apparently advantaged over high biomass species such as Z. capricorni.

6.5.2.3. Seagrass recovery at site E5

The results of the exclosure experiments appear to be supported by the changes in seagrass abundance at site E5, one of the sites monitored for 21 months to describe the seasonality of seagrasses (Chapter 4).

When first sampled, (July 1988), site E5 was composed of H. ovalis and H. spinulosa only. However, the sediment contained large amounts of dead and decomposing rhizomes of Z. capricorni (2-3 times the amount of live Halophila rhizomes (Figure 6.12). Based on the rate of decomposition of Zostera rhizomes (Kenworthy and Thayer, 1984; section 4.3.1.4), Z. capricorni was probably the dominant species at this site 3-6 months prior to sampling. The subsequent succession followed the pattern seen in the intensively 'grazed' exclosures. These facts suggest that the site may have been intensively grazed by dugongs 3-6 months prior to the commencement of monitoring. If so, the period of dominance by H. ovalis, following major grazing disturbance, is brief. It dominated between 9-12 months after the presumed grazing, but had been out-competed by H. spinulosa within 12-15 months after the grazing (Figure 6.12).

6.6. Discussion

6.6.1. Where and how dugongs feed

6.6.1.1. Feeding site selection

In Moreton Bay, dugongs fed mostly on seagrasses of low to moderate biomass growing on sandy substrates in depths ranging from 1.5 to 2.5 m deep at high tide (mean = 1.9 m). They also fed on ascidians living in or on finer sediments in deep water (7 m).

The 13 feeding sites at which seagrass biomass was measured had a median total biomass of 86.2 g/m^2 and a median shoot density of 2,569 shoots/m^2. However, these figures overestimate the amount of seagrass at most feeding sites, as few sites in areas of sparse seagrass were sampled. For example, during aerial surveys, 23.9% of dugongs were seen on the Turtle Bank and northern Claire's Complex, but only 14.3% of feeding sites (sites 5, 13 and 15) were located here. This area was under-sampled because the very sparse seagrass (253 shoots/m^2; Table 6.2b; see also Figure 3.2) combined with the almost continuous grazing of the area usually made it impossible to identify a particular feeding site.

Sixty-three percent of dugong groups (n = 115) encountered on seagrass were in areas with sparse vegetative cover. Only 10% were in areas of dense seagrass (Table 6.12).

Within the range of sediments available in the study areas, neither grain size nor compaction appear to influence the dugongs' choice of feeding sites. The amount of shell in the sediment, however, may have had an influence: the dugongs fed more frequently at sites with a low shell content (Figure 6.2).

Shells, especially those from large cockles and thick-shelled gastropods are not easily crushed and may have sharp edges, and this could be an impediment to efficient chewing. The mouth parts of the dugong are highly modified, and the whole oral cavity may function to masticate seagrasses (Lanyon, 1991). The occlusion, during the chewing cycle, of the large horny pads on the mandible, tongue, premaxilla and palate both macerates and transports the seagrass backwards towards the teeth and throat (Lanyon, 1991). The frequent occurrence of hard and sharp shells tangled amongst the seagrass rhizomes and roots may prevent uniform occlusion of the pads, and hence, reduce the efficiency of the maceration and transportation processes. If this effect is significant, the dugongs may choose to either avoid areas with a high content of hard shells, or modify their grazing mode, so they process less sediment. An example of the latter response may have occurred at feeding site 28-1. This site contained a significantly larger amount of shell than any other feeding site (Figure 6.2; 2,438 g shell material/m^2, SE = 336), and the dugongs removed 85.1% of the above-ground biomass of H. uninervis, but only 28.0% of the below-ground biomass.

6.6.1.2. How dugongs forage

There is no definitive account of how dugongs actually ingest seagrass. Their retiring nature and habit of stirring clouds of sediment when feeding have conspired to prevent any revealing underwater observations in the wild. From an ecological perspective, this is not a serious restriction as the dugongs leave ample signs of their feeding.

When feeding, dugongs apparently swim slowly forward, perhaps supported by their forelimbs (Anderson and Birtles, 1978; Barnett and Johns, 1976; Jarman, 1966), removing seagrass leaves, and (usually) rhizomes, as they go. In the process, they typically produce meandering feeding trails (Figure 6.6b), analogous to those produced by foraging walruses (Nelson and Johnson, 1987), which have similar callused areas on the ventral edges of their flippers (H. Marsh, pers. comm.).

When grazing on seagrasses on the sandy substrates in Moreton Bay, dugongs produced feeding trails (at four sites) with an average length of 2.27 m (at a fifth site they averaged 4.79 m). Anderson and Birtles (1978) recorded average feeding trail lengths of 2.94 m and 8.05 m from two beds of seagrass growing on sandy mud at Shoalwater Bay, Queensland (22.35° S, 150.5° E). At the latter seagrass bed, Wake (1975; also reported in Heinsohn et al., 1977) described feeding trails as 1-5 m long. Although there was no correlation between seagrass density and feeding trail lengths at four sites in Moreton Bay, very short feeding trails (30-50 cm) were observed in an area of S. isoetifolium with an exceptionally high shoot density.

The width of feeding trails in Moreton Bay (11.8 cm at a typical site and 22.7 at another site) appears to be substantially narrower than those at Shoalwater Bay (19-25 cm, Wake, 1975; 23.3 cm, Anderson and Birtles, 1978). This difference is probably due to differences in substrate type. At the Shoalwater Bay sites, the sediments were primarily mud or sandy mud, while those in Moreton Bay were composed of well sorted siliceous sand. When feeding in sandy substrates, dugongs may have to constrict their rostral disk to make it easier to push through the sediment. In soft mud, such a response may not be necessary, and the dugongs could flare their upper lip, allowing them to maximise their cropping width. The width of feeding trails recorded by Anderson and Birtles (1978; 23.3 cm) corresponds with the width of the rostral disc of dead dugongs at Townsville (males: 22.3 cm, SE = 1.05; females: 22.2 cm, SE = 1.24; Spain and Heinsohn, 1975).

Regional differences in feeding trail morphology should not be surprising as dugongs have been reported to employ a variety of foraging methods. Aragones (1990) described circular patches (20-25 cm and up to 1 m diameter) in seagrass made by foraging dugongs in the Philippines. The scars left by feeding dugongs in Kenya (Jarman, 1966) are intermediate between such patches and typical feeding trails reported from Australia.

In Moreton Bay, dugongs have a flexible repertoire of foraging methods, concomitant with their varied diet. When feeding on seagrass with a dense rhizome mat, or when feeding on S. pulchra, the dugongs usually surface graze, removing little below-ground material. Otherwise, when feeding on seagrass, they furrow graze, harvesting rhizomes and roots as well as leaves. Anderson (1981) described two modes of grazing by dugongs in Shark Bay. One is equivalent to furrow grazing, while the other is an extreme form of surface grazing. In that case, the dugongs strip the clusters of leaves from the tall wiry stems of Amphibolis antarctica.

The Moreton Bay dugongs also forage on two distinct forms of solitary ascidians. Free-standing forms (eg. Polycarpa obscura, P. pigmentata) attach to shell fragments and sit above the substrate, while a buried form (P. fungiformis) normally exposes only the tips of its siphons inconspicuously at the surface (pers. obs.). My observations suggest that dugongs locate and excavate these buried ascidians, burst open their very tough tests and ingest the soft internal tissue. Freshly opened tests of P. fungiformis were found adjacent to craters (40 cm wide by 15 cm deep) in the substrate in a deep (7 m) area of the Rous Channel where seagrass was absent, but where I observed dugongs surfacing in a manner that suggested that they were feeding. Anderson (1989) also reports that circular craters, approximately 55 cm wide and 9 cm deep, were made by the dugongs as they apparently foraged for a thin-shelled burrowing mussel (Botula vagina) and possibly a sea pen (Virgularia sp.).

Florida manatees apparently feed on seagrass in a different manner to dugongs. Individual Florida manatees often produce elliptical feeding patches, which in one study, averaged 27 m^2 in area (Lefebvre and Powell, 1990). Manatees may also produce a type of elongated scar that looks superficially like a dugong's feeding trail. These scars can be about 45 cm wide and extend for one to several metres (Provancha and Hall, 1991).

Unlike dugongs, Florida manatees do not always feed on the rhizomes of seagrasses, and when they do, they forage differently than dugongs. Packard (1984) described two types of seagrass feeding by Florida manatees: 'grazing', where only the leaves are taken and 'rooting', where the manatees use their forelimbs to help dig out the rhizomes. (Despite early reports [Gohar, 1957], there is no credible evidence that dugongs use their forelimbs in this manner). Some studies of manatee feeding report only 'grazing' (Hartman, 1979; Provancha and Hall, 1991) while others report both types of feeding (Lefebvre and Powell, 1990; Zieman, 1982 cited in Thayer et al., 1984).

As the rhizomes of seagrasses can be a rich source of carbohydrates (Dawes and Lawrence, 1980; Lanyon, 1991), it is perhaps surprising that Florida manatees do not feed on them more consistently. The explanation may partly lie in the animals' contrasting anatomies. Due to the extreme deflection of its rostrum, the dugong is highly adapted to bottom feeding (Domning, 1976), while the Florida manatee has a less deflected snout (Domning, 1982) and may not be so well adapted to feeding on the bottom. Lyn Lefebvre (pers. comm.), believes that Florida manatees do frequently feed on rhizomes, although this feeding is relatively inefficient, and the feeding scars can be difficult to identify.

Feeding trail 'efficiency'

At 12 feeding sites, including two that were surface grazed, the following proportions of seagrass components were harvested along feeding trails: 86% of the number of shoots; 91% of the above-ground biomass; 59% of the rhizome biomass and; 25% of the root biomass. Over 93% of S. pulchra colonies were removed along trails at another site (Table 6.5).

The total biomass of seagrass was reduced by an average of 53.1% at the 12 sites (65.2% at the seven sites not dominated by Z. capricorni). Wake (1975; also presented in Heinsohn et al., 1977) estimated that dugongs removed an average of 63-67% (two occasions) of the total biomass of seagrass along feeding trails through a sparse bed of Z. capricorni growing on mud. At the same location, Anderson and Birtles (1978) estimated that 58.6-78.2% (results of two methods) of seagrass shoots were removed along feeding trails. In Moreton Bay, I estimate that dugongs feeding on Z. capricorni thin removed an average of 83% of shoots, 92% of above-ground biomass, 36% of rhizome biomass and 21% of root biomass (Table 6.5).

In as much as their different foraging methods can be compared, manatees in Florida remove seagrass as effectively as dugongs. Within beds of Halodule wrightii and Syringodium filiforme, manatees removed 83-94% of shoots, 79-95% of shoot biomass and 46-67% of the biomass of rhizomes and roots (Lefebvre and Powell, 1990). In a separate study at the same location, manatees removed 93% and 96% of the total biomass of S. filiforme at two sites (Packard, 1984). The grazing of Thalassia testudinum was more variable, and there is some evidence that the manatees surface graze this species, unless the rhizomes have already exposed by currents or other factors (Lefebvre and Powell, 1990). In a different study, the percentage cover of S. filiforme in experimental plots was reduced by 90% by leaf-grazing manatees (Provancha and Hall, 1991).

6.6.2. Diet

6.6.2.1. Foods eaten

Seagrass

Z. capricorni was the most abundant seagrass identified in the faeces of dugongs in Moreton Bay. Leaf material of Z. capricorni occurred in 88% of samples, making up 11% of their wet weight. By comparison Halophila (H. ovalis and H. spinulosa) occurred in 79% of samples, but constituted only 3% of their bulk (Table 6.8). From this data it would seem that dugongs feed more on Z. capricorni than Halophila species. However, this deduction contradicts other data (see below), and illustrates the major disadvantage of faecal analysis as a method of reconstructing the diet of a herbivore. Different species, and parts of the same species, are digested at different rates because they contain varying levels of digestion inhibitors such as fibre and secondary metabolites (Lanyon, 1991; Thayer et al., 1984). Therefore, the relative abundance of material in faecal samples is not necessarily a true reflection of consumption (Barker, 1986; Holechek et al., 1982; Vavra and Holechek, 1980). In the absence of correction factors derived by feeding diets of known composition to captive animals (Barker, 1986; Holechek et al., 1982), these biases can be serious.

Rhizome material in the faeces could not be identified to species or genus, so indications of specific preferences could be inferred from the leaf material only. However, the leaves of different species undergo differential digestion. The proportion of faecal samples in which Z. capricorni leaves were present (88% of samples), was similar to the proportion for all the other species of seagrass combined (92%), however, leaf material of Z. capricorni was over three times more abundant than the leaf material of all of the other species combined (Table 6.8). Of five species of seagrass examined by Lanyon (1991), dugongs digested H. ovalis the most efficiently, while Z. capricorni was the least digestible. The leaves of Z. capricorni contain a significantly higher level of fibre than any of the other species of seagrass occurring in Moreton Bay (Lanyon, 1991), and this probably accounts for their relatively low digestibility and hence, their high abundance in the faecal samples (Lanyon, 1991).

The signs of dugong feeding demonstrated that dugongs have some capacity to feed selectively and that they often avoid Z. capricorni. When Z. capricorni was intermixed with other species of seagrass, no selectivity was shown and it was furrow grazed, along with the other species. However, when Z. capricorni occurred in dense mono-specific stands, the dugongs tended to avoid the broad-leafed morph (Table 6.14). Sometimes they would graze surrounding seagrasses intensively, but all feeding trails would end at the very edge of the Z. capricorni patch (Table 6.15).

In contrast to Z. capricorni broad, Z. capricorni thin was sometimes selected by grazing dugongs, but apparently only when it was in fruit (Table 6.16). Usually, it was then surface grazed (Table 6.6). The stomach contents of three dugongs that died during the study support these findings. Z. capricorni predominated in the stomachs of MB-1 (in one of the three distinct zones) and MB-2 (Table 6.10). In both cases the Z. capricorni was the thin-leafed morph and rhizomes made up a small proportion of the total volume. Furthermore, it is probable that the Z. capricorni grazed by dugong MB-1 was fruiting, based on the date of the dugongs death (10 October; Table 6.10) and the fruiting phenology of Z. capricorni (Table 6.16; Wassenberg, 1990).

Algae

Early records of the diet of dugongs imply a dependence on algae (Annandale, 1905; Hirasaka, 1932; Mani, 1960). However, these records do not mention the presence of seagrass, suggesting possible misidentification. Moreover, these records were usually based on the stomach or gut contents of a single animal. Subsequent studies indicate a relatively insignificant role for algae in the diet of dugongs. Algae were found in only three of the faecal samples from Moreton Bay (6.3%), occurring at trace levels in two of these. Similarly, Marsh et al. (1982) found algae in 51% of 95 stomach contents, but usually in small amounts (<2% volume). Algae were present in only 6.7% of mouth samples collected from 102 dugongs by Johnstone and Hudson (1981). Under some circumstances, however, dugongs may be able to supplement their diet with algae. Spain and Heinsohn (1973) and Marsh et al. (1982) have documented an increase in the consumption of algae following a severe cyclone which presumably reduced the standing crop of seagrass (Heinsohn and Spain, 1974). During the period 3.5 to 11 months after the cyclone, nine of 12 netted dugongs had fed on large quantities of Sargassum. Three stomachs contained more than 73% algae.

Although not quantified, the dugongs of Moreton Bay showed a pronounced avoidance of the alga Caulerpa mexicana (pers. obs.). This was most conspicuous at AO's shoal, where 95% of seagrass shoots from an area of >16 ha were removed by intensive grazing (Area 3, Table 6.17). Small patches of C. mexicana (30-50 cm diameter) were left ungrazed by the dugongs, and during the period of monitoring the highest biomass of seagrass occurred in these patches.

The dugongs also appeared to eschew seagrass that carried a large amount of epiphytic algae. At feeding site 17, the dugongs avoided an area of H. spinulosa that was covered with a blanket of epiphytic algae (Table 6.13), but fed on an immediately adjacent area (mostly H. ovalis) that carried little algae. Similarly, at site 21-2, the leaves of S. isoetifolium supported a thick growth of epiphytic algae, while the adjoining patches of H. uninervis and Z. capricorni were relatively clean. Only 15 of 127 feeding trails occurred in the S. isoetifolium, and 11 of these were located along the edges of the S. isoetifolium patch, where the abundance of the algae was lowest.

Invertebrates

Dugongs have the opportunity to feed on many sessile invertebrates. However, macro-invertebrates have not previously been reported as a significant component of their diet. A review of earlier studies of the contents of dugong stomach and mouth samples indicates that invertebrate material is rarely encountered (Table 6.20). These studies concluded that dugongs are wholly vegetarian, occasionally ingesting invertebrate material incidentally with seagrass (Marsh et al., 1982; Lipkin, 1975; Spain and Heinsohn, 1973). The incidence of 'other' invertebrate material (unidentified worms, worm tubes, and colonial hydrozoans) in the

Moreton Bay faecal samples (33% occurrence, 2% abundance) and in the samples from tropical Australasia (29% occurrence, 1.2% abundance) accords with this conclusion. Only Anderson's (1989) observations of six dugongs apparently foraging for invertebrates indicate that dugongs may deliberately feed on animals.

The incidence of ascidians in the faecal samples from Moreton Bay clearly demonstrates that the diet of dugongs from this area contrasts significantly with that of dugongs from the other areas studied. The stalks of the colonial ascidian S. pulchra was present in 69% of faeces and made up an average of 29% of their wet weight. The mantles of solitary ascidians occurred in 27% of samples and constituted 20% of their bulk (Table 6.8). Ascidians of one form or another occurred in 73% of faecal samples collected in Moreton Bay and, averaged across all samples, constituted 25.5% of their bulk.

Dugongs were clearly feeding selectively on these ascidians. The density of S. pulchra was significantly higher, and the density of seagrass significantly lower, in the vicinity of the dugong feeding trails than in the surrounding area. This suggests that the dugongs were deliberately feeding on the ascidians, rather than ingesting them incidentally while feeding on the seagrass. The dugongs removed over 93% of S. pulchra colonies along feeding trails. Some faecal samples were composed almost entirely (99% of wet weight) of the stalks of S. pulchra.

Solitary ascidians were relatively uncommon on the seagrass banks, occurring much more frequently in deeper water where very little or no seagrass grows (pers. obs.). Hence the presence of the remains of solitary ascidians in 27% of faecal samples further suggests deliberate selection.

Further evidence for deliberate carnivory by dugongs is provided by the stomach contents of dugong MB-1. This stomach was highly stratified, each stratum apparently representing different feeding locations. One zone was composed entirely of a gregarious polychaete (family Chaetopteridae) and its tubes (Table 6.10). No seagrass material was mixed with the polychaetes, so there is no possibility of their being ingested incidentally.

While dugongs in Moreton Bay selectively fed on ascidians and some polychaetes, they apparently avoided eating other invertebrates. They frequently excavated a soft sea pen (Cavernularia obesa) and a large anemone (Stoichactis sp.) but did not eat them (I often found them rolling about in, or adjacent to recent feeding trails). Similarly, small gastropods were abundant on the seagrass banks, yet only a few tiny fragments of their shells were found in the faecal samples.

Like dugongs, Florida manatees are generally considered to be wholly herbivorous, the ingestion of invertebrates occurring incidentally to their normal feeding (Hartman, 1979). However, manatees are also known to consume ascidians, as they were found in the gastrointestinal tracts of at least 23 of 43 manatees examined as a result of an unusual die-off in 1982 (O'Shea et al., 1991). Furthermore, deliberate carnivory by manatees has been documented in northern Jamaica (Powell, 1978), where some manatees deflesh small fish caught in fixed gill nets.

6.6.2.2. Diet preferences

Several studies of dugong diet, based on stomach or mouth samples, have demonstrated that dugongs feed on a wide variety of seagrasses (Gohar, 1957; Heinsohn and Birch, 1972; Johnstone and Hudson, 1981; Lipkin, 1975; Marsh et al. 1982; Wake, 1975). In the absence of information about the availability of the different seagrasses, however, these studies provide measures of usage and cannot elucidate preference (Johnson, 1980). Most authors have noted, however, that dugongs appear to prefer the smaller, more delicate, often low-biomass species of seagrasses (Heinsohn and Birch, 1972; Lipkin, 1975; Marsh et al. 1982; Wake, 1975). My data from Moreton Bay support these impressions. Dugongs fed most frequently on low-biomass communities composed of species of Halophila and H. uninervis thin (relatively small, delicate species). They generally avoided high biomass sites dominated by Z. capricorni broad (a comparatively large, tough species) and fed infrequently on the high biomass patches of S. isoetifolium and H. uninervis broad (intermediate sized species, relative to the others).

I have been able to rank the seagrasses in Moreton Bay according to the apparent preferences of the dugongs. This ranking is based on my frequency of encounter with feeding dugongs in different seagrass communities, the relative abundance of the species of seagrass in areas accessible to the dugongs, and the signs left by feeding dugongs. The ranking is most applicable to the summer/autumn seasons, when the abundance of seagrass is greatest (section 4.3.2.2) and, therefore, the dugongs are likely to be most selective (Ellis et al., 1976 and references therein). The proposed ranking, in order of decreasing preference is:

H. ovalis ≥ H. uninervis thin > H. spinulosa >
S. isoetifolium ≥ H. uninervis broad > Z. capricorni broad

The high ranking of H. uninervis thin results from its invariable association with H. ovalis, and may not be warranted.

Z. capricorni thin, H. decipiens and C. serrulata have not been ranked. Z. capricorni thin is a seasonally preferred species. The dugongs selected it when it was fruiting. They also fed on at least two tracts of it during winter, possibly because of their proximity to the warm waters of South Passage. At most times it was not eaten (in the East study area).

Although I have no evidence that dugongs feed on C. serrulata in Moreton Bay, I am unable to conclude that dugongs do not like it. C. serrulata has a very restricted distribution in Moreton Bay (Figure 3.1), and this may account for the low level of use. During aerial surveys, only two dugongs (out of 10,326 sighted) were seen within 500 m of the C. serrulata meadows. The apparent avoidance of C. serrulata may have also been related to the relatively high level of human disturbance (boat mooring, oyster leases and fish netting) around the C. serrulata meadows.

H. decipiens tends to occur in relatively deep water (Community H6, Figure 3.5) and can be grazed when the other species are not accessible. As the dugongs did not have to choose between this and the other species, I am unable to assign it a relative rank.

6.6.2.3. Nutritional basis for diet selection

Herbivores can be limited by food quantity (Haukioja et al., 1983; McNaughton and Georgiadis, 1986), although food quality is frequently more important (McNaughton and Georgiadis, 1986; Owen-Smith and Novellie, 1982). Large herbivores may select their diet on the basis of its nutritional quality and/or the rate at which it can be eaten (Cooper and Owen-Smith, 1986; Kenney and Black, 1984; Lewin, 1985; McNaughton and Georgiadis, 1986; Owen-Smith and Novellie, 1982).

In nutritional terms, nitrogen is one of the most important components of a herbivore's diet. Nitrogen is necessary for protein synthesis, and while carnivores obtain it from protein-rich animal tissue, herbivores obtain their nitrogen from plants. Because nitrogen is frequently in short supply in plants (Mattson, 1990; White, 1985), it is often used as an indicator of the nutritive value of herbage.

Other dietary components can also be important. Cooper and Owen-Smith (1986) found that food selection by kudus (Tragelaphus strepsiceros), impalas (Aepyceros melampus) and domestic goats was influenced more strongly by the abundance of condensed tannins and fibre (which can act as digestion inhibitors) than by the abundance of nitrogen, suggesting that energy availability was more important than nitrogen availability under the test conditions.

The energy intake per bite can also be a critical property of a grazer's food source. At low rates of intake per bite, herbivores may starve in the midst of apparent plenty (Haukioja et al., 1983; Lewin, 1985). Hungry domestic sheep selected food on the rate at which it could be consumed rather than its digestibility (Kenney and Black, 1984).

The fact that dugongs in Moreton Bay avoid areas of high seagrass biomass, where the rate of food consumption could be maximised, indicates that nutritional values other than gross energy intake are important in determining their dietary preferences.

Several nutritional studies have partitioned the constituents of seagrasses according to their potential digestibility, making them relevant to interpreting the dugongs' diet (Anderson, 1986; Birch, 1975; Bjorndal, 1979, 1980; Duarte, 1990; Lanyon, 1991). However, these studies are not compatible, as they examined a disparate selection of species using a variety of analytical techniques (Lanyon, 1991; Thayer et al., 1984). Lanyon's (1991) examination of the nutritional status of inter-tidal seagrasses from the Townsville area, which is the most comprehensive study to date, included five of the nine species/morphs found in Moreton Bay, and therefore, will be used to interpret the dietary preferences of the Moreton Bay dugongs.

Lanyon (1991) measured total nitrogen, available nitrogen, soluble carbohydrate, tannins and fibre in the following seagrasses: Halodule (narrow), H. uninervis broad, C. serrulata, H. ovalis and Z. capricorni broad. The category Halodule (narrow) contained H. uninervis thin and/or Halodule pinifolia, and was probably equivalent to the H. uninervis thin morph that occurs in Moreton Bay.

Chemical composition varied widely between the different species examined by Lanyon (1991), as well as between different components (above- and below-ground) of the same species. Furthermore, different morphs of the same species (H. uninervis broad and Halodule (narrow)) contained different levels of some components, demonstrating the importance of differentiating ecomorphs of species (Lanyon, 1991).

Nitrogen

The seagrasses examined contained low levels of total nitrogen (compared with most terrestrial grasses). The leaves of different species contained 1.4-1.91% nitrogen, while the roots and rhizomes contained less than half these values. Generally, less than 20% of the total nitrogen was considered to be available to a consumer, based on in vitro extraction.

Lanyon (1991) established the following ranking of the seagrasses, ordered by decreasing nitrogen availability (in vitro):
H. ovalis > Halodule (narrow) > H. uninervis broad >
C. serrulata > Z. capricorni.

This list matches the rank of dugong-preferred species (H. ovalis ≥ H. uninervis thin > H. uninervis broad > Z. capricorni broad; after removal of species not considered by Lanyon, 1991), suggesting that the dugongs in Moreton Bay feed selectively to maximise nitrogen intake.

Soluble carbohydrate

Lanyon (1991) found that the seagrasses, and particularly the rhizomes, were high in soluble carbohydrates. The highest levels occurred in Halodule (narrow), which contained up to 25.8% DM soluble carbohydrate in the rhizomes and roots and 6.4% in the leaves. With the exception of Halodule (narrow), there was little variation in the level of soluble carbohydrates in the leaves of species (3.28-3.84%).

The following list ranks the seagrasses examined in order of decreasing levels of soluble carbohydrate in the below-ground components:

Halodule (narrow) > H. uninervis broad > C. serrulata > Z. capricorni > H. ovalis.

As seagrass carbohydrate occurs in forms that are readily digestible by dugongs (mainly as monosaccharide sugars such as glucose and fructose, and as disaccharide sucrose; Lanyon, 1991), rhizomes appear to be an important energy source for dugongs.

Tannins

Tannins can deter feeding and have been suggested as a basis of food choice by some animals (Cooper and Owen-Smith, 1986; Freeland and Janzen, 1974;

Westoby, 1978) and condensed tannins can act to inhibit nitrogen digestion (Lanyon, 1991). Tannin levels varied between species. H. ovalis and Z. capricorni had no detectable levels of condensed tannins. If tannins are an effective defence against seagrass herbivores, dugongs would be expected to select species with low levels of condensed tannins.

In order of increasing levels of tannins, the seagrasses examined by Lanyon (1991) are:

H. ovalis ≤ Z. capricorni < Halodule (narrow) < H. uninervis broad < C. serrulata.

With the exception of Z. capricorni, the levels of condensed tannins correlated negatively with their order of preference. The fact that Z. capricorni contained no detectable tannins, but was avoided by dugongs suggests that while tannins may influence diet choice, they are not the predominant determining factor.

Fibre

The levels of fibre in seagrasses are relatively low compared with terrestrial grasses (Lanyon, 1991). In order of increasing fibre levels (neutral detergent fibre) in the leaves, Lanyon's seagrasses are ranked:

H. ovalis < Halodule (narrow) < C. serrulata < H. uninervis broad < Z. capricorni.

Based on fibre content of the roots and rhizomes, the ranking changes to:

C. serrulata < Halodule (narrow) < H. ovalis < H. uninervis broad < Z. capricorni.

When other measures of fibre (ADF, hemicellulose, cellulose, lignin) are considered, the rankings of H. ovalis and Z. capricorni leaves do not alter and Z. capricorni always contained the highest levels in the rhizomes and roots.

Lanyon (1991) also examined the fibre levels (NDF) in seagrass from four other locations in eastern and northern Australia. Included were H. spinulosa and S. isoetifolium, which also occur in Moreton Bay. Perhaps due to their disparate origins as much as the small number of samples, the results were quite variable. It was apparent, however, that both S. isoetifolium and H. spinulosa contain relatively low levels of NDF. S. isoetifolium contained lower levels of fibre than any other species occurring in Moreton Bay, while the level in H. spinulosa placed it at a similar ranking to H. ovalis and Halodule (narrow). At each of the four locations, Z. capricorni had the highest levels of fibre.

Z. capricorni seeds

Dall et al. (in press) examined the composition of the seeds of Z. capricorni from Moreton Bay. They contained substantially more soluble carbohydrate than the non-reproductive parts of the seagrasses (60% cf. 15-32%), less fibre (22% cf. 42-63%) and similar nitrogen (although different methods were used). The seeds of Z. capricorni are a richer food source than any of the vegetative parts of any of the seagrasses examined by Lanyon (1991).

After studying the functional morphology of dugong mouthparts, Lanyon (1991) considers that the dugong is atypical of most other hindgut fermenters because of its unspecialised dentition. As a result, she asserts that the dugong has become specialised for a low fibre diet of seagrasses that fracture easily (providing access to cell contents). She considered that the dugong "no longer appears equipped to handle the fibre levels intrinsic to seagrass species such as Zostera capricorni." (Lanyon, 1991, p 224). In light of these findings, it is not surprising that Z. capricorni broad ranks last on the preference list of dugongs in Moreton Bay, and that it is usually avoided when in grows in pure stands (but see below). The apparent aversion for this species may be exacerbated by the relatively slow rate of decomposition of Z. capricorni rhizomes, which results in a build up of fibrous dead rhizomes amongst the live rhizomes (see section 4.3.6).

Due to the generally low levels of nitrogen in seagrasses, Lanyon (1991) considered that dugongs may have difficulty meeting their nitrogen requirements, at least at certain times of the year. By selecting for seagrasses with high levels of available nitrogen, the dugongs could maximise their intake of this limiting nutrient. Accordingly, the order of preferred seagrasses correlates with the ranking of seagrasses in terms of nitrogen availability. Selective feeding on invertebrates may also be a strategy of dugongs in Moreton Bay to increase their nitrogen intake (see below).

Lanyon (1991) also studied the 'breakability' of seagrasses in relation to their digestibility. Available nitrogen and fibre fermentation was found to be a function of particle size, which is likely to be related to the ease with which it fragments when subjected to mechanical stress. She found marked variation in 'breakability' between species. The most preferred species, H. ovalis and H. uninervis thin (probably equivalent to Lanyon's Halodule (narrow)) break relatively easily, while Z. capricorni is the least breakable species. Hence, the order of preference of seagrasses correlates with their overall digestibility.

The dugongs in Moreton Bay appeared actively to avoid some macro-algae (most noticeably Caulerpa mexicana) as well as seagrasses supporting heavy growths of epiphytic algae. Florida manatees may also avoid caulerpoid algae when grazing (Provancha and Hall, 1991). Based on the relatively large particle size of algal fragments in the stomachs and intestines of dugongs, Lipkin (1975) and Marsh et al. (1982) concluded that dugongs are poorly adapted to utilise algae as a food source. Lipkin (1975) thought it probable that dugongs could not adequately chew algae due to their more flexible consistency. This observation supports Lanyon's (1991) hypothesis, that dugongs need to select relatively breakable foods to compensate for their unspecialised dentition.

Algae may also be avoided because of the presence of secondary metabolites, which occur in extremely high levels in some species (Norris and Fenical, 1982; Steinberg, 1984). Paul and Fenical (1986) have described the herbivore-deterrent abilities of algae in the order Caulerpales (containing C. mexicana). Hay et al. (1987) found that the application of secondary compounds, extracted from a variety of algae, to leaves of the palatable seagrass Thalassia testudinum significantly reduced the level of consumption by coral reef herbivores. Even plants living near algae that produce secondary compounds are less susceptible to predation by herbivores because of their proximity to a distasteful plant (Hay, 1986). This finding is in accord with the observed high density of H. ovalis amongst ungrazed patches of C. mexicana, when the surrounding areas had been thoroughly grazed. Interestingly, tunicates can also contain significant levels of secondary compounds. These are mostly (90%) amino-acid derived, nitrogen based metabolites (Van Alstyne and Paul, 1988).

The dugongs of Moreton Bay appear to select their diet on the basis of low fibre, high available nitrogen (and presumed digestibility), and low secondary metabolites. By feeding on Z. capricorni thin while it is in fruit, they may also be selecting for high energy levels.

6.6.3. Causes and consequences of foraging strategies

6.6.3.1. Stresses and feeding strategies

The abundance and productivity of seagrasses follows a seasonal pattern, with most species showing highest levels in summer/autumn and lowest levels in winter/spring (section 4.3.2.2; Figure 4.1). The level of nutrients in seagrasses can also vary seasonally (Dawes and Lawrence, 1980).

Total nitrogen is one of the most seasonally-variable constituents. Lanyon (1991) found that total nitrogen varied as much as two-fold between a wet season (summer/autumn) high and a dry season (winter/spring) low. Each of the five species examined by Lanyon (1991) showed this pattern. Lanyon (1991) also found considerable inter-year variation in nitrogen levels in seagrasses. No other constituent showed a significant seasonal change in abundance. In Florida, protein levels in Thalassia testudinum and Syringodium filiforme were highest in summer and autumn and lowest in spring and winter, although Halodule wrightii did not display a seasonal change (Dawes and Lawrence, 1980). Harrison and Mann (1975) found that in Zostera marina, which had a spring growing season, nitrogen peaked during winter/spring. Similarly, in Moreton Bay, where Z. capricorni has a winter/spring growing period (section 4.3.2.2), leaf-nitrogen levels are significantly higher in winter than summer (Boon, 1986). These results indicate that nitrogen levels are highest in seagrasses during their period of seasonal growth. This is consistent with the finding that nitrogen and soluble carbohydrate levels are highest, and fibre levels lowest in newly formed leaves, and that these decline (fibre increases) as the leaves age (Bjorndal, 1980; Harrison and Mann, 1975; Pirc and Wollenweber, 1988; Zieman et al., 1984).

These data indicate that not only is the abundance of seagrasses in Moreton Bay at its lowest levels during winter/spring (excepting Z. capricorni), but that the level of nitrogen within those seagrasses is also at a minimum during that period. Taken together, it is clear that the total availability of nitrogen is most restricted, and may be limiting, in winter/spring. After studying nitrogen pools in seagrasses and interstitial water in Moreton Bay, Boon (1986) concluded that nitrogen was the nutrient most likely to limit growth of seagrasses. When interstitial nitrogen is reduced, so is the level of nitrogen in seagrass tissues (Thayer et al., 1984). Based on the levels of available nitrogen in seagrasses, Lanyon (1991) considered that dugongs could have seasonal problems meeting their maintenance requirements.

Nutrient limitations occur in terrestrial grazing systems. "A vague, qualitative state of undernutrition has almost universally been identified as an important factor influencing the dynamics of all those African herbivore populations ...." (McNaughton and Georgiadis, 1986, p. 55). In the Serengeti, large standing crops of grass are maintained through the year, but crude protein levels drop below maintenance requirements during the dry season. Consequently, herbivore requirements exceed available nutrients for 1-4 months each year (Sinclair, 1975). As a result, wildebeest lose condition, and the rate of mortality increases (Sinclair, 1975). Stelfox and Hudson (1986) demonstrated that the proximate determinant of body condition of Thomsons's and Grants's gazelles was forage quality, while the ultimate factor was the rainfall pattern that determined the growth of vegetation. The dry-season plight of Serengeti grazers is exacerbated by heat stress and a shortage of drinking water (Stelfox and Hudson, 1986).

Dugongs in Moreton Bay may also suffer the compounding affects of seasonal stresses. Winter is not only the period of low, probably limiting nitrogen availability, but also the period of cold water temperatures. Like African ungulates that offset dry season stresses by spending more time in shade or by moving to and from water (Sinclair, 1977), dugongs offset the effects of cold water by regularly migrating out of the Bay to warm oceanic water. This migration entails a round trip of 15-40 km, and the dugongs have to fast for hours to days as they take refuge in the warm water east of South Passage (section 5.4.2.2). There is also some evidence that during this period, the dugongs forage on seagrasses that are normally not preferred, presumably because they are some of the closest seagrasses to the warm-water refuge and because they are inundated with relatively warm water during the flood tide (section 5.4.2.2). Predicably, these stresses appear to have had a negative impact upon the condition of the dugongs.

This loss of condition was evident during the pursuit and capture of dugongs for tagging. The six dugongs captured in early winter (June 1988), and the three captured during summer (January 1989) were strong and robust. In sharp contrast, the nine dugongs captured during spring (October 1988) lacked stamina and were apparently in poor condition. Four of these nine dugongs had to be released before they were tagged as they showed signs of severe exhaustion and may have drowned. No such problems were encountered with the early-winter- and summer-caught dugongs.

The dugongs caught in spring had just endured three months of water temperatures, on the seagrass banks, that were below the apparent threshold of dugongs (section 2.2) and were currently experiencing the annual minimum of seagrass (and presumably nitrogen) abundance. By contrast, the dugongs captured in early winter would have had substantial fat reserves accumulated through the previous three months of maximum seagrass growth. By summer, the dugongs would have been in good condition, due to the abundance of nutritious new seagrass growth, and the return of warm water conditions.

The dugongs in Moreton Bay cope with these environmental and nutritional stresses by incorporating a migration into their regular movements, and by dietary specialisation to maximise the quality of their food. The dugongs appear to employ several strategies to maximise the quality of their diet.

A principal strategy appears to maximise nitrogen intake while minimising consumption of fibre and this is achieved at a variety of scales, commensurate with their capacity for selective grazing. At the system level, the dugongs select particular seagrass communities to feed in. Hence, they feed most frequently in seagrass communities dominated by the species of seagrass with the highest levels of total and available nitrogen: the species in seagrass community group H (Halophila species and H. uninervis thin; Figure 5.5). At the community level, the dugongs are adept at selecting between patches of different species. Consequently, they usually attempt to minimise their intake of the fibrous, and relatively indigestible seagrass Z. capricorni broad by avoiding dense patches (Table 6.14). However, at the individual plant level, their potential for selective grazing is limited by their wide muzzle (relative to the plants; Janis, 1988; Jarman, 1974) and by their feeding mode whereby they remove seagrass from long narrow strips (up to 14 m long; Heinsohn and Marsh, 1977) that invariably sample many plants. As a result, they consume Z. capricorni broad in accordance with its abundance where it occurs inter-mixed with other species.

The avoidance of seagrass communities dominated by Z. capricorni broad may have been largely seasonal. The aerial survey and tracking data indicate that during winter and spring the dugongs may in fact select for seagrass communities dominated by this species (Figures 5.6 and 5.9). In some, if not most cases, the dugongs actually selectively fed on patches of other species in these communities. However, the rafts of leaves of Z. capricorni broad that were commonly encountered in the study area suggested that the dugongs were also feeding on Z. capricorni. The dugongs may feed on this species because of the nutritional deficiencies of the more preferred species during winter and spring.

Z. capricorni is the only seagrass in Moreton Bay to deviate from the pattern of a summer/autumn growth peak, producing shoots in winter, with maximum leaf production in spring (section 4.3.2.2). Consequently, nitrogen levels in the leaves of Z. capricorni are highest in winter (Boon, 1986), when they would be lowest in the other species of seagrass. Furthermore, the level of fibre in the new leaves of Z. capricorni would be relatively low (Bjorndal, 1980; Harrison and Mann, 1975). The new growth of even highly fibrous plants may be satisfactory food (Polisini and Boyd, 1972). Hence, the dugongs are able to exploit the different growth seasonality of Z. capricorni to help compensate for the deficiencies of the normally preferred species during winter and spring.

The dugongs may also fed selectively on beds of Z. capricorni thin during spring (Figures 5.6 and 5.9). They may have been attracted by the new leaves, but it is more likely that they were seeking the abundant carbohydrate-rich seeds. Two grazed beds contained an estimated 7.2 g soluble carbohydrate/m^2. This compares with 2.7 g/m^2 for vegetative parts alone. These seeds were probably efficiently harvested as 96-97% of above-ground biomass was removed from feeding trails (Table 6.6). Because of their high level of digestible carbohydrate (60%; Dall et al., in press), these seeds are also harvested by a normally carnivorous prawn (Penaeus esculentus) in Moreton Bay (Wassenberg, 1990; Wassenberg and Hill, 1987).

Dugongs in Moreton Bay also maximise their intake of protein, by deliberately foraging on selected sessile invertebrates. The colonial ascidian (S. pulchra) that comprised over 20% of the wet-weight of faecal samples was consumed significantly more during spring than during summer or winter. However, in the absence of data on the seasonal availability of this opportunistic ascidian (Shepherd, 1983), the seasonal pattern of consumption may not necessarily reflect selection by dugongs.

The consumption of solitary ascidians showed no seasonality. Consumption of these ascidians during summer and autumn, when seagrasses are relatively abundant may simply reflect a learned feeding habit (Ellis et al., 1976 and references therein). Alternatively, these data may suggest chronic nutrient deficiency. Such a situation may not be unusual. In the Serengeti, 75% of grass samples were deficient in sodium, to the extent that they were a potential limitation on the quality of the grazer's food (McNaughton, 1989). In the wild many ungulates chew bones and cast antlers (Clutton Brock et al., 1982).

From an examination of stomach and faecal samples from tropical Australasia, as well as a review of the literature on dugong diets, it appears that dugongs in other, more tropical areas, do not deliberately consume animal material. This anomaly may be explained by a possible (but undocumented) difference in the nitrogen content of tropical and sub-tropical seagrasses. However, it is more probable that this omnivory by the dugongs in Moreton Bay is a response to seasonal nutritional stress combined with the physiological and energetic stresses caused by cold water temperatures in winter at the edge of the species' range. Dugongs in lower latitudes do not have to contend with cold water temperatures. The only other record of dugongs deliberately foraging on invertebrates comes from Shark Bay (Anderson, 1989), which is also at the southern limit of the dugong's range (in western Australia). Anderson (1986) considers that these dugongs may be forced into a negative energy budget during winter.

As a further strategy to maximise the quality of their diet, the dugongs of Moreton Bay may have adopted a foraging strategy that maximises the availability of preferred seagrasses (see below).

6.6.3.2. 'Cultivation' grazing by dugong herds

In Moreton Bay, dugongs feed in large herds (half the dugongs seen on aerial surveys were in herds of >140; section 7.3.1) that often return to the same sites to feed for periods of up to four weeks or more (Table 5.4). By feeding in large herds, and by concentrating their grazing in restricted areas, the dugongs in Moreton Bay can have major impacts on the seagrass communities. Like other herbivores (Huntly, 1991 and references therein), dugongs can significantly alter community structure and dynamics (see below). Most importantly, from a nutritional point of view, they can alter the species composition and nutrient status of extensive seagrass meadows. I refer to the concentrated grazing by large herds as 'cultivation' grazing.

Grazing by dugongs can constitute a major disturbance to seagrass meadows. At favoured locations the crisscrossing feeding trails can cover virtually 100% of the site. Two such areas monitored in Moreton Bay, Areas 2 and 3, occupied approximately 75 and 41 ha, respectively. At Area 3 the density of seagrass shoots was reduced by 95% when it was first grazed (Figure 6.6) and by 92% six months later, after the site had partly recovered. On the second grazing the above-ground biomass was reduced by 96%, while 71% of the below-ground biomass was grazed. At the 75 ha Area 2, grazing reduced shoot density by 65%, above-ground biomass by 73% and below-ground biomass by 31%.

The loss of seagrass can be greater than these initial measurements indicate. At Area 2, the biomass of seagrass rhizomes continued to decline for some two months after grazing had ceased (Figure 6.7), probably due to the eventual death of small, unviable segments of rhizome created by the dense network of feeding trails. At Area 3, the sudden reduction in the number of seagrass shoots resulted in substantial pressure from grazing gastropods, and further loss of seagrass (pers. obs.). Similar post-disturbance mortality, resulting from an imbalance of prey and predator populations has also been documented on a coral reef (Connell and Keough, 1985).

Terrestrial herbivores can have similarly dramatic impacts. For example, large herds (over half a million) of migrating wildebeest (Connochaetes taurinus albojubatus) remove 85% of green biomass as they pass through areas (McNaughton, 1976). The disturbance caused by dugong grazing differs from that of most terrestrial herbivores, however, because a substantial proportion of the below-ground plant material is also consumed.

I estimate that the dugongs in Moreton Bay disturb a cumulative total of 68 km^2 of seagrass per year by their feeding (see Appendix 7.2 for details). This represents 84% of the area of seagrass used by dugongs in the East study area. This grazing disturbance, however, was not evenly distributed. Just as grasslands grazed by large mammalian herbivores are often a mosaic of heavily and lightly grazed areas (Bakker et al., 1983; Coppock et al., 1983b; Heitschmidt et al., 1989; McNaughton, 1984; Willms et al., 1988), some areas of seagrass were used almost continuously, while others were virtually never used. Hence, the return interval, the average time between disturbances (Sousa, 1984), was very variable (see below).

Recovery

Despite the intensity and areal extent of the disturbance that can result from grazing by dugong herds, the recovery of the seagrasses can be rapid (Figures 6.7 and 6.8). This recovery is facilitated by the way dugongs feed as well as the growth characteristics of seagrasses. Rather than each dugong methodically cropping all the seagrass in a series of adjoining small areas, the dugongs produce countless meandering feeding trails, like as many randomly oriented lines. Despite the great density of these trails, small tufts of seagrass survive (Figure 6.6c). These represent an ungrazable reserve (Noy-Meir, 1975), and are the key to the resilience of the seagrass meadows in the face of intensive grazing disturbance. The key to the rapid recovery after grazing has ceased is the even distribution of these tufts of seagrass.

At Area 3, the remnants of seagrass that survived continued grazing suggest an ungrazable reserve of 110-120 shoots/m^2 (about 4% of pre-grazing density). These shoots, aggregated in small tufts, sometimes linked by surviving rhizomes, act as nuclei, able to expand to fill the bare gaps once grazing ceases. Usually the tufts are much less than a metre apart, so modest expansion by thousands of tufts can rapidly reclaim the near-barren substrate of large areas. The vegetative morphology of seagrass facilitates this regrowth. The high density of feeding trails fragments the seagrass rhizomes and interrupts their growth pattern, allowing determinate shoots to be converted to indeterminate shoots, and thus promoting proliferative growth (Tomlinson, 1974).

The recovery of seagrass from grazing disturbance contrasts with recovery from disturbances caused by sedimentation, water or ice scour or some form of die-off (Poiner et al., 1989; Short, 1983; pers. obs.). The critical difference is the effective patch size: the minimum distance between survivors capable of regeneration (Connell and Keough, 1985). Hence, while an area of >50 ha may be severely disturbed by dugong grazing, the effective patch size is perhaps less than 0.5 m^2, and recovery is rapid. The area of seagrass meadows affected by sedimentation or die-off (such as sites W2 and E2 monitored to document seasonality; section 4.3.1) can be considerably smaller, but these sites are often uniformly impacted and must recover by ingrowth from the edges, or by colonisation by seeds or other propogules. Under these circumstances recovery can be a very slow process (Birch and Birch, 1984; Clarke and Kirkman, 1989; Poiner et al., 1989). Recovery of disturbed sites within meadows of terrestrial grasses are also determined by similar patch-size related processes (Coffin and Lauenroth, 1988).

Recovery of heavily grazed seagrass meadows is not invariably rapid. Area 3 was grazed twice during the 300 days of monitoring (Figure 6.8), and the difference between the two recoveries provides a useful insight into the dynamics of this herbivore-plant system. After the initial grazing, no dugongs were seen at the site for months, and recovery was rapid, even though the growing season was unfavourable. Despite a favourable growing season following the second grazing incident, the recovery of the seagrass was suppressed by continued low-intensity grazing. These data suggest that subsequent to a major grazing disturbance, a seagrass community may not recover, and can be held in a low level steady-state by a minimal level of continued grazing (Noy-Meir, 1975).

6.6.3.3. Effect of grazing disturbance on species composition

The exclosure experiments showed that a disturbance, like intensive dugong grazing, can alter the relative abundance of seagrasses. The disturbance encouraged H. ovalis, while it retarded the expansion of Z. capricorni and H. spinulosa.

Site E5, which was located in the same seagrass community as the exclosure experiments (community ZB5), had apparently been heavily grazed 3-6 months prior to the commencement of monitoring, and the changes in the relative abundance of the seagrasses reflected the pattern seen in the exclosure experiment that simulated intensive grazing. Based on the relative abundance of its dead rhizomes, Z. capricorni had dominated the site prior to grazing. Nine to twelve months after grazing, the site was dominated by H. ovalis. After a further 15 months, the site was dominated by H. spinulosa (Figure 6.12).

H. ovalis is a pioneer species (Brouns, 1987b) and its presence is a good indication of past disturbance (Birch and Birch, 1984). Z. capricorni is the dominant and climax species in Moreton Bay. Little is known of the community ecology of H. spinulosa. In Moreton Bay, H. ovalis is the dugongs' most preferred species, while Z. capricorni is their least preferred species during most of the year. Zieman (1976) describes several examples of disturbed patches of the climax Thalassia testudinum being colonised by Halodule wrightii (referred to as H. beaudettei), which also is a pioneer species (Phillips and Menez, 1988).

In some seagrass communities, therefore, intensive and repetitive grazing of areas by large herds of dugongs appears to disrupt the normal succession. As a consequence, the area and biomass of the dugongs' favoured species of seagrass is increased, at the expense of their least preferred species.

No changes in species composition were detected following disturbance by grazing at Areas 2 and 3. Prior to grazing, Area 3 was already a virtually pure stand of the H. ovalis, while the areas monitored at Area 2 were composed solely of H. uninervis broad, a species adapted to disturbance (Birch and Birch, 1984; Brouns, 1987b).

Herbivores have been demonstrated to have a major impact on the species composition of plant communities in a wide variety of habitats, ranging from seagrasses (Ogden, 1976; Tribble, 1981), macro-algae (Hinds and Ballantine, 1987; Lubchenco, 1978), micro-algae (Hunter, 1980; Hunter and Russell-Hunter, 1983); salt marshes (Smith, 1983), natural grasslands (Coppock et al., 1983a; Edroma, 1989; Jaramillo and Detling, 1988; Lock, 1972; McNaughton, 1979; McNaughton and Georgiadis, 1986), grasslands grazed by domestic stock (Bakker et al., 1983; Ellis et al, 1976; Heitschmidt et al., 1989; Ralphs et al., 1990; Willms et al., 1988) and woodlands (Laws, 1970; Owen-Smith, 1988). Some plant species require disturbance, such as grazing, to allow them to successfully compete (Edroma, 1989; McNaughton, 1979; Smith, 1983). In the absence of grazing, tall grasses can overgrow and shade shorter species to the point of exclusion (Edroma, 1989). Interception of light is an important factor in the successional replacement of the seagrass Syringodium filiforme by the taller growing Thalassia testudinum (Williams, 1987). Both Z. capricorni and H. spinulosa are tall species of seagrass, compared with H. ovalis, and competition for light may also be a factor governing succession in these species in Moreton Bay.

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

6.6.3.4. Effect of grazing disturbance on forage quality

The nutritional quality of plants can increase following injury, including damage caused by herbivory (Karban and Myers, 1989). The shoot nitrogen concentration of terrestrial plants (Coppock et al., 1983a; Kilcher, 1981) and seagrasses (Harrison and Mann, 1975; Zieman et al., 1984) generally declines as the plants age and mature. However, heavy or prolonged grazing often increases the shoot nitrogen content of grasses (Bakker et al., 1983; Coppock et al., 1983a; Heitschmidt et al., 1989; Jaramillo and Detling, 1988; McNaughton, 1984). Productivity can also be significantly increased by grazing (Cooper, 1973; Hunter, 1980; Hunter and Russell-Hunter, 1983; Jaramillo and Detling, 1988; McNaughton, 1976, 1979, 1984, 1985). Georgiadis et al., (1989) found that the response to defoliation of grasses of the African savanna was contingent upon a complex interaction of factors, and that grass production was stimulated by grazing, under the conditions that normally exist at the time of grazing.

Seagrasses respond to cropping or clipping of leaves by increasing nitrogen levels and decreasing levels of lignin or ash in new growth (Bjorndal, 1980; Dawes and Lawrence, 1979; Thayer et al., 1984; Zieman et al., 1984). Thus, 'cultivation' grazing allows dugongs to maximise the quality of their diet not only by increasing the area of nutritionally superior, early successional species of seagrass, but by increasing the nutritional quality of grazed seagrasses generally. This is achieved by maintaining meadows in an immature, rapidly growing state, much as practised by green turtles (Bjorndal, 1980; Ogden et al., 1980; Thayer et al., 1984; Zieman et al., 1984) and some large terrestrial herbivores (Edroma, 1989; McNaughton, 1985).

6.6.3.5. Why feed in large herds?

McNaughton (1984) argues that the modification of the vegetation physiognomy is the most important impact of grazing ungulates. By reducing the grass canopy height and increasing tillerage, the green biomass is concentrated closer to the ground, and the grazers increase their food yield per bite. Food yield per bite can be critical to meeting the nutritional needs of large mammalian herbivores under some circumstances (Chacon et al., 1978; Stobbs, 1973). Grazing by dugongs does not directly increase the food per bite, or food per dive, as the intense grazing tends to lower the biomass of seagrass. However, by disturbing large areas at a time, and thus encouraging uniform recovery, often of a favoured species, 'cultivation' grazing achieves the equivalent of McNaughton's (1984) biomass concentration. If the dugongs did not feed in large herds, their dispersed feeding trails would not modify the species composition (Figure 6.11), and the nutritionally superior regrowth vegetation would be widely dispersed and could not be as efficiently harvested.

McNaughton (1984) postulates that gregariousness in grazing animals may have evolved because of the increase in foraging efficiency that accrues to individuals as a result of changes in vegetation structure that follow herd grazing. He argues that while lone animals could achieve the same increase in forage yield per bite, by concentrating their grazing in a small area, such animals would be highly subject to predation. Predation , however, has not prevented green turtles

(Bjorndal, 1980; Ogden et al., 1980; Thayer et al., 1984; Zieman et al., 1984) and damselfish (Hinds and Ballantine, 1987; Kamura and Choonhabandit, 1986; Sammarco, 1983) from maintaining individual foraging patches of seagrass and algae, respectively. Solitary dugongs are prevented from 'cultivation' grazing, not by predation, but by their mode of feeding. Just as their habit of removing seagrass from long narrow strips ensures the survival of many strips and patches of seagrass, thus facilitating rapid recovery from grazing, it also prevents individual dugongs from significantly disturbing a substantial single area of seagrass. Thus, individual dugongs could not change the species composition of the seagrass bed, nor concentrate the regrowth into distinct patches so that it could be efficiently harvested. Only by feeding in large herds could dugongs achieve a sufficient density of feeding trails, over a large enough area to achieve these results. Florida manatees, with muzzles less specialised for bottom feeding, do not produce feeding trails in the manner of dugongs. Instead, when they feed on seagrasses, they crop circular patches (mean 27 m^2). Interestingly, there is some evidence that they return to the same patches in subsequent years (Lefebvre and Powell, 1990), so they may also effect a 'cultivation' affect.

6.6.3.6. Optimal foraging

The following is a summary of my interpretation of the causes and consequences of dietary selection by dugongs in Moreton Bay.

Dugongs in Moreton Bay operate under three principal constraints:

1. their staple food, seagrass, has a low nitrogen content
2. unlike other large hind gut fermenters, they are ill-equipped to cope with a high fibre diet
3. they are at the edge of their species' range and the low water temperatures during winter subject them to particular physiological stresses, resulting in additional energetic demands.

The Moreton Bay dugongs counter these constraints by maximising the quality of their diet. To this end, they appear to:

1. maximise intake of nitrogen
2. minimise consumption of fibre
3. avoid foods, particularly algae, with high levels of secondary metabolites
4. maximise carbohydrate intake seasonally.

These strategic aims are achieved by:

1. feeding in seagrass communities with the highest proportion of nutritionally superior species
2. feeding selectively on seagrass patches within communities
3. feeding on selected invertebrates
4. varying their diet seasonally to capitalise on periods of seed and shoot production of Z. capricorni, and possibly ascidian blooms
5. practising 'cultivation' grazing, thereby:
    - maximising abundance of nutritionally superior, early successional species of seagrass
    - concentrating regrowth in particular areas, allowing the dugongs to feed more efficiently on new growth with low fibre, high nitrogen levels.

These interactions between the dugongs and the seagrasses are not fully explained by the predictions of any particular optimal foraging model. Rather, the components of several models can be seen to be operating. Early models that presupposed that energy intake was the critical currency for measuring diet selection (Pyke et al., 1977) would appear to be less appropriate than Westoby's (1974) 'optimization model' or Owen-Smith and Novellie's (1982) 'clever ungulate' model. The former predicts that a large generalist herbivore should aim to achieve the best nutritional balance within a fixed total bulk of food, while the latter reasons that ungulates should maximise the intake of the most limiting nutrient at the time of foraging. The range of criteria upon which the dugongs appear to base their selection of food, and the variety of approaches they seem to employ to achieve this selection, suggests a complex, dynamic relationship that is beyond the scope of the simple models.

It is apparent that 'cultivation' grazing is a critical component of the dugongs' dietary optimisation. Given the nutritional benefits that can accrue from 'cultivation' grazing, why don't dugongs in other areas also feed in large herds? This issue will be considered in Chapter 7.

Table 6.1. Summary details of dugong feeding sites studied in Moreton Bay. Seagrasses present (ordered by decreasing relative abundance at each site), approximate number of dugongs recently seen in the area, and the parameters measured are presented for each site. 'Y' indicates that the parameter was measured.

Feeding site	Seagrasses[1]	Dugongs seen in area #, Days ago	Characteristics measured						
			Sediment, Shell	Seagrass abundance			Feeding trail dimensions	Grazing efficiency	Evidence for selective grazing
				% cover	Shoot density	Biomass			
1	Hs, Ho		Y	Y					Y
2	Hs, Zc, Ho	30, 2	Y	Y					Y
3	Hs, Ho	20-30, 0	Y	Y					Y
4	Hs, Ho	15-30, 0	Y	Y					Y
5	Ho, Hu, Hs	50-100, 0	Y	Y	Y				
6	Ho, Hs	50, 1	Y	Y			Y		Y
7	Ho, Hu	200, 1	Y	Y					
8	Ho, Hs	50, 2	Y	Y					
9	Ho, Hu	100, 1	Y		Y				Y
10	Ho, Hs	30, 0	Y		Y				
11	Ho, Hs	83, 3	Y		Y				
12	Ho, Hu	223, 2	Y		Y		Y		
13	Ho, Hu	50, 0	Y		Y		Y		
14	Hu				Y		Y		Y
15	Ho	20, 0	Y		Y				
16	Hu, Ho		Y		Y	Y		Y	
17	Ho, Zc, Hs		Y		Y		Y		
18	Zc	100, 0	Y		Y	Y		Y	
19	Ho	100, 0			Y	Y		Y	
20	Ho	150, 0	Y		Y	Y		Y	
21-1	Hu		Y		Y	Y			
21-2	Si		Y		Y	Y			
22	Zc, Hu, Ho	162, 8	Y		Y	Y		Y	
23	Ho, Hs	64, 2			Y	Y		Y	
24-1	Zc, Ho							Y	Y
24-2	Zc, Ho				Y	Y		Y	Y
25	Zc, Hu				Y	Y		Y	
26	Ho, Hs, Hu				Y	Y		Y	
27	Sp, Hd				Y			Y	
28-1	Hu		Y		Y	Y		Y	Y
28-2	Si				Y	Y		Y	Y
29	Zc	1, 1	Y						

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[1] Hd: H. decipiens; Ho: H. ovalis; Hs: H. spinulosa; Hu: H. uninervis; Sp: Sycozoa pulchra; Si: S. isoetifolium ; Zc:Z. capricorni.

Table 6.2a. Abundance of seagrasses at the subset of dugong feeding sites at which overall percentage cover and relative abundance of each species were measured.

		Total % cover		Relative abundance (%)							
Feeding site	Quadrats (n)	mean	SE	*Halophila spinulosa* mean	SE	*Halophila ovalis* mean	SE	*Halodule uninervis* mean	SE	*Zostera capricorni* mean	SE
1	20	5.9	0.5	54.3	8.4	45.7	7.0				
2	20	27.0	2.9	36.5	8.8	31.5	8.5			32.1	10.1
3	20	12.4	1.3	61.0	5.5	39.0	5.5				
4	20	22.3	2.4	55.0	6.0	45.0	6.0				
5	20	1.0	0.1	6.3	4.5	83.3	7.2	10.4	6.1		
6	20	17.5	1.7	49.3	4.6	50.7	4.6				
7	20	2.7	0.5			87.3	3.8	12.7	3.8		
8	20	14.2	1.5	39.0	5.6	61.0	5.6				

Table 6.2b. **Abundance of seagrasses and and the ascidian Sycozoa pulchra at the subset of dugong feeding sites at which shoot (and stalk) density was measured in the field and in the laboratory.**

Feeding site #	Quadrats (n)	Total		Halophila spinulosa		Halophila ovalis		Halodule uninervis		Zostera capricorni		Syringodium isoetifolium		Halophila decipiens		Sycozoa pulchra	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Density (shoots and/or stalks/m²) : Field count																	
5	20	263	35	25	19	210	38	29	18								
9	42	1974	93			1176	82	798	68								
10	60	657	37	151	20	506	34										
11	75	668	30	298	32	370	21										
12	17	2949	139	3	3	2837	136	110	36								
13	75	261	31			194	24	67	16								
14	16	2008	128					1958	142	50	30						
15	60	236	26			229	25	7	4								
16	19	370	59			129	37	241	48								
17	60	936	36	171	40	515	43	4	2	247	40						
20	21	274	59			274	59										
21-1	10	720	135					720	135								
23	18	1187	111	373	79	794	112					20	20				
26	18	1587	117	540	74	980	103	67	33								
27	23	1327	297	63	34	12	11							177	52	1077	319
Shoot density (shoots/m²): Lab count																	
16	19	566	90			194	59	372	73								
18	16	8953	346					450	217	8503	418						
19	20	319	87			281	75	38	26								
20	21	480	79			480	79										
21-1	10	2569	334					2569	334								
21-2	10	7275	552									7275	552				
22	19	5141	550			234	93	512	165	4395	523						
23	18	1727	163	480	95	1221	184					27	27				
24-2	20	634	101			21	21			613	118						
25	6	9514	990			70	70	282	151	9161	1027						
26	18	2261	182	700	99	1427	163	133	67								
28-1	10	2875	678					2875	678								
28-2	10	8732	1215									8732	1215				

Table 6.2c. Abundance of seagrasses at the subset of dugong feeding sites at which above- and below-ground biomass were measured.

Feeding site #	Quadrats (n)	Total		Halophila spinulosa		Halophila ovalis		Halodule uninervis		Zostera capricorni		Syringodium isoetifolium	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Above-ground biomass (g/m²)													
16	19	4.29	0.83			2.47	0.77	1.82	0.34				
18	16	44.73	2.71					0.57	0.28	44.16	2.82		
19	20	2.37	0.67			2.27	0.64	0.10	0.07				
20	21	4.85	0.89			4.85	0.89						
21-1	10	13.01	2.83					13.01	2.82				
21-2	10	208.10	14.30									208.10	14.30
22	19	17.42	1.90			0.59	0.21	1.31	0.60	15.51	1.89		
23	18	36.91	3.03	13.86	2.83	22.34	2.96					0.71	0.71
24-2	20	1.70	0.34			0.01	0.01			1.69	0.03		
25	6	105.00	10.99			0.07	0.07	1.02	0.59	103.92	11.47		
26	18	32.53	2.71	15.77	2.76	16.00	1.66	0.76	0.39				
28-1	10	16.90	4.69					16.90	4.69				
28-2	10	96.40	16.05									96.40	16.05
Below-ground biomass (g/m²)													
16	19	9.98	1.64			3.41	1.15	6.57	1.44				
18	16	182.17	15.72					5.03	2.43	177.14	16.75		
19	20	12.08	2.53			11.65	2.45	0.44	0.27				
20	21	7.89	1.51			7.89	1.51						
21-1	10	179.10	26.24					179.10	26.24				
21-2	10	348.60	17.89									348.60	17.89
22	19	68.82	5.19			1.49	0.58	3.60	1.11	63.72	4.92		
23	18	30.82	2.48	11.02	2.06	18.79	2.14					1.00	1.00
24-2	20	17.92	3.51			0.01	0.01			17.91	3.51		
25	6	244.45	24.68			0.38	0.26	4.90	3.08	239.17	25.45		
26	18	44.59	2.94	13.17	2.59	27.91	3.05	3.52	1.95				
28-1	10	137.60	13.98					137.60	13.98				
28-2	10	237.80	36.35									237.80	36.35

Table 6.3. The proportion of seagrass shoots counted in the field as a percentage of those counted in the same samples in the laboratory.

Species	n	Field count as percentage of lab count mean	SE
Ungrazed seagrass			
H. spinulosa	28	80.0	3.6
H. ovalis	67	68.3	3.0
H. uninervis	31	55.7	5.8
Seagrass in feeding trails			
H. ovalis	17	92.1	4.3
H. uninervis	13	67.1	8.2

Table 6.4. **Results of analyses of variance testing for differences in the mean abundance of seagrass in quadrats along, and adjacent to, feeding trails at 12 sites. Data were square root transformed.**

Factor	df	MS	F	p
Shoot density				
Position[1,2]	1	117361	839.37	0.0001
Site[1,3]	11	17138	122.57	0.0001
Position*Site	11	3474	24.85	0.0001
Error	362	140		
Total	385			
Shoot biomass				
Position[1,2]	1	1314	1291.55	0.0001
Site[1,3]	11	90	88.14	0.0001
Position*Site	11	52	50.75	0.0001
Error	362	1		
Total	385			
Rhizome biomass				
Position[1,2]	1	488.4	243.8	0.0001
Site[1,3]	11	440.4	219.9	0.0001
Position*Site	11	48.7	24.3	0.0001
Error	362	2.0		
Total	385			
Root biomass				
Position[1,2]	1	27.0	23.22	0.0001
Site[1,3]	11	272.3	234.01	0.0001
Position*Site	11	11.2	9.64	0.0001
Error	362	1.2		
Total	385			

[1] Fixed factor

[2] Inside feeding trail or adjacent to feeding trail

[3] Sites: 16, 18, 19, 20, 22, 23, 25, 26, 241, 242, 281, 282

Table 6.5. Percentage of different parts of different species of seagrass (and *Sycozoa pulchra*) removed by dugong from feeding trails. Only data from sites where the particular species were dominant or co-dominant are presented.

Species	Number of sites	Percentage removed							
		Density		Biomass (g/m^2)					
		(Shoots or stalks/m^2)		Above-ground		Rhizome		Root	
		mean	SE	mean	SE	mean	SE	mean	SE
H. spinulosa	2	99.3	0.5	100.0	0.0	97.4	0.4	80.6	10.4
H. ovalis	5	90.9	1.9	90.2	3.1	77.8	4.8	33.9	15.4
Z. capricorni	5	82.7	7.1	91.5	4.8	35.5	13.7	20.7	8.2
H. uninervis	2	71.7	1.8	79.1	4.2	46.3	12.9	7.9	5.6
S. isoetifolium	1	97.6		99.0		96.5		47.1	
Sycozoa pulchra	1	93.2							

Table 6.6. Variation among sites in the proportion of shoots, rhizomes and roots of *Z. capricorni* removed along surface and furrow-grazed feeding trails.

Site	Seagrass abundance adjacent to feeding trails				Reduction of seagrass abundance along feeding trails (%)				Observed method of grazing
	Shoot density	Biomass (g/m^2)			Shoot density	Biomass (g/m^2)			
	(shoots/m^2)	Shoot	Rhizome	Root	(shoots/m^2)	Shoot	Rhizome	Root	
18	8503	44.2	177.1		51.1	70.4	5.8		surface
25	9161	103.9	123.8	115.4	88.2	97.0	25.6	13.6	surf[2] + furr
24-1	6871	47.8	83.4	78.3	89.2	95.8	40.8	44.6	surf + furr
22	4651	16.5	28.1	37.6	91.8	95.5	75.6	24.6	furrow
24-2	613	1.7	8.6	9.3	93.1	98.8	0[1]	0[1]	furrow

[1] Low value is an artefact due to the low biomass of seagrass

[2] surf = surface; furr = furrow

Table 6.7. Result of analysis of variance testing for a difference between methods of estimating the abundance of material on microscope slides of dugong faeces. Twenty-one faecal samples were assessed by both methods.

Factor	df	MS	F	p
Method[1,2]	1	116.9	0.34	0.5605
Category of material[1,3]	2	1211.0	3.53	0.0317
Method*Category	2	28.3	0.08	0.9132
Error	120	343.1		
Total	125			

[1] Fixed factors

[2] Method (1) and Method (2): see text

[3] Sycozoa pulchra, Zostera capricorni and Halophila spp.. Due to the high proportion of unidentifiable rhizome, these categories were independent.

Table 6.8. Occurrence (percentage of samples containing item) and abundance (mean percentage of each sample composed of item) of material in 48 faecal samples collected from dugongs in Moreton Bay.

	Occurrence	Abundance (%)					
	(%)	in samples in which items occured			in all samples		
		mean	SE	range	mean	SE	range
Rhizome	100.0	61.5	5.4	0.5-100	61.5	5.4	0.5-100
Seagrass leaf							
Z. capricorni	87.5	10.6	2.9	0.5-74.5	9.3	2.6	0-74.5
Halophila spp.	79.2	2.9	1.0	0.1-34	2.3	0.8	0-34
H. uninervis	22.9	0.5	0.1	0.2-1.5	0.1	0.04	0-1.5
S. isoetifolium	6.3	0.25			0.02	0.01	0-0.3
Algae	6.3	7.0	5.5	0.2-20.4	0.4	0.4	0-20.4
Ascidians							
S. pulchra	68.8	29.3	6.1	0.2-99	20.2	4.6	0-99
Solitary	27.1	19.7	6.0	0.3-68.7	5.3	2.1	0-68.7
Other[1]	44.0	2.0	0.7	0.02-13	0.9	0.3	0-12

[1] Worms, worm tubes, shells, colonial hydrozoans, seagrass seeds.

Table 6.9. Results of analyses of variance testing for temporal differences in the abundance of dietary items in 48 faecal samples from dugongs from in Moreton Bay.

		Seagrass leaves					
		Z. capricorni			Halophila spp.		
Factor	df	MS	F	p	MS	F	p
Year (Yr)[1,2]	1	264.0	1.02	0.3178	67.1	2.32	0.1354
Season (Seas)[1,3]	2	616.6	2.39	0.1043	59.2	2.05	0.1420
Yr*Seas	2	1619.4	6.27	0.0041	103.3	3.57	0.0370
Error	42	258.3			28.9		
Total	47						

		Ascidians					
		S. pulchra			Solitary		
Factor	df	MS	F	p	MS	F	p
Year (Yr)[1,2]	1	977.7	1.18	0.2830	456.6	2.49	0.1220
Season (Seas)[1,3]	2	3427.4	4.15	0.0227	251.6	1.37	0.2645
Yr*Seas	2	839.4	1.02	0.3709	408.3	2.23	0.1203
Error	42	826.6			183.3		
Total	47						

[1] Fixed factors
[2] 1988-9 and 1989-90
[3] Winter, spring and summer

Table 6.10. Stomach contents of three dugongs from Moreton Bay.

Stomach	Rhizome as % of volume	Relative abundance (%) of identifiable material				
		Zostera capricorni	Halophila ovalis	Halodule uninervis	Syringodium isoetifolium	Poly-chaetes
MB-1[1] Zone 1	20	99	1	0	0	0
Zone 2	60	30	70	0	0	0
Zone 3	0	0	0	0	0	100
MB-2[2]	1	99	1	0	0	0
MB-3[3]	90	10	80	5	5	0

[1] 2.88 m adult female died 10 October 1988
[2] 3.00 m adult male died 22 May 1989
[3] 3.0 m adult female died July 1989

Table 6.11. Occurrence (percentage of samples containing the item) and abundance (mean percentage of each sample composed of item) of non-seagrass material in 33 stomach and 15 rectal samples from north Queensland and Papua New Guinea. Microscopic and parasitic invertebrates were not considered.

	Occurrence (%)	Abundance (%)			
		in samples in which items occured		in all samples	
		mean	SE	mean	SE
Ascidian	6.2	0.7	0.27	0.04	0.12
Holothurian	2.1	7.8	0	0.16	1.10
Sponge	6.2	1.1	0.36	0.07	0.18
Worm	2.1	0.1	0	trace	
Worm tube	12.5	0.3	0.07	0.03	0.05
Colonial hydrozoan	2.1	0.02	0	0.01	0.003
Unidentified invertebrate	6.2	0.6	0.23	0.03	0.10
Filamentous algae	10.4	1.0	0.29	0.10	0.16
Macro-algae	6.2	0.2	0.15	0.01	0.05
Wood	2.1	0.1	0	trace	

Table 6.12. Species of seagrasses, and the relative abundance of seagrass, recorded at locations where 115 herds were encountered on vegetated areas of the East study area in Moreton Bay.

Seagrass present[1]	Number of herds			
	Seagrass abundance			Total
	Sparse	Medium	Dense	
Ho, Hs	25	13	7	45
Ho	17	4	3	24
Ho, Hu	9	2	-	11
Hs	5	3	1	9
Ho, Hu, Hs	7	-	-	7
Ho, Hs, Zc	-	7	7	7
Ho, Zc	4	-	-	4
Ho, Hu, Zc	1	2	-	3
Hd, Hs	3	-	-	3
Ho, Hs, Si	1	-	-	1
Hu, Zc	-	1	1	1
Total	72	32	11	115

[1] Ho: H. ovalis; Hs: H. spinulosa; Hu: H. uninervis; Zc: Z. capricorni;
Si:S. isoetifolium; Hd: H. decipiens

Table 6.13. Frequency and relative frequency of seagrasses along feeding trails, contrasted with their relative frequencies at the feeding sites, and the results of Chi square goodness of fit tests comparing the frequency distributions. Also results of an analysis of variance testing for a difference between the density of S. pulchra colonies adjacent to feeding trails and generally at site 27.

Feeding site	n[1]	Species	Along feeding trails		At site	Difference[2]	Chi[3] square	df	p
			Frequency	Relative frequency					
1	68	H. spinulosa	37	54.41	54.25	+0.2	0.006	1	0.9368
		H. ovalis	31	45.59	45.75	-0.2			
2	153	H. spinulosa	95	62.09	36.45	+25.6	30.28	2	0.0000
		H. ovalis	44	28.78	31.50	-2.7			
		Z. capricorni	14	9.15	32.05	-22.9			
3	74	H. spinulosa	42	56.76	60.95	-4.2	0.3633	1	0.5467
		H. ovalis	32	43.24	39.05	+4.2			
4	108	H. spinulosa	53	49.07	55.00	-5.9	0.7925	1	0.3733
		H. ovalis	55	50.93	45.00	+5.9			
6	94	H. spinulosa	38	40.43	49.25	-8.8	1.543	1	0.2142
		H. ovalis	56	59.57	50.75	+8.8			
9	57	H. ovalis	34	59.65	59.57	+0.1	0.000	1	1.0000
		H. uninervis	23	40.35	40.43	-0.1			
17	580	H. spinulosa	12	2.07	18.25	-16.2	114.5	3	0.0000
		H. ovalis	457	78.79	54.96	+23.8			
		Z. capricorni	101	17.41	26.36	-8.9			
		H. uninervis	10	1.72	0.43	+1.3			
			Density of colonies (stalks/m²)				F	df	p
			Beside feeding trails		At site				
27	31, 23	S. pulchra	3618		1077		9.28	1, 52	0.0036

[1] Number of points at which seagrass was identified along feeding trails

[2] Difference between relative frequency along feeding trail and relative frequency at site

[3] Comparing frequency of species along edge of feeding trails with expected frequency of species at site. Expected frequency = relative frequency * n

Table 6.14. Density of feeding trails (estimated by line transects) in areas of dense Z. capricorni and in surrounding areas of seagrass at four feeding sites in the East study area.

Feeding site	Seagrass	Number of transects	Area of feeding trails as a percentage of total area
2	H. spinulosa, Z. capricorni, H. ovalis	10	28.8
	Z. capricorni patch	8	1.7
14	H. uninervis	8	6.6
	Z. capricorni patch	8	0.0
24-2	sparse Z. capricorni	40	16.5
	dense Z. capricorni	40	1.1

Table 6.15. Biomass of seagrass in cores along three short transects straddling the boundary between an ungrazed Z. capricorni dominated seagrass patch within a grazed H. uninervis meadow. Cores were 20 cm apart. Core 1 was located in the Z. capricorni patch, cores 2 and 3 in the H. uninervis.

Species	Component	Biomass (g/m²)					
		Core 1		Core 2		Core 3	
		mean	SE	mean	SE	mean	SE
Z. capricorni	Above-ground	80.1	16.6	0.0		0.0	
	Below-ground	115.7	15.2	0.0		0.0	
H. uninervis	Above-ground	27.6	5.7	3.4	1.4	2.4	1.0
	Below-ground	144.4	34.6	62.8	18.0	82.9	26.6

Table 6.16. Abundance of reproductive shoots in intertidal areas of Z. capricorni thin grazed by dugongs.

Feeding site	Date	Shoot density (shoots/m²)				Reproductive shoots as % of total
		Total		Reproductive		
		mean	SE	mean	SE	
18	22-8-89	8502	418.4	267.7	66.0	3.1
22	12-9-89	4651	558.5	?		?
24-1	10-11-89	6871	423.5	1035.0	119.0	15.1
24-2	10-11-89	613	117.7	10.6	10.3	1.7
25	9-1-90	9161	1027	1022.0	251.2	11.2

Table 6.17. Abundance of seagrass at feeding areas before and after they were intensively grazed by dugongs and the percentage of seagrass removed. Area 3 was grazed twice during the monitoring period. 3-1 and 3-2 refer to the first and second grazing of Area 3.

Area	Species	Seagrass abundance				Reduction
		Before		After		(%)
		mean	SE	mean	SE	
		Shoot density (shoots/m^2)				
Area 1	All	1587.3	116.7	213.3	37.2	86.6
	H. ovalis	980.4	103.3	115.3	20.6	88.2
	H. spinulosa	504.2	74.1	76.9	21.9	85.8
	H. uninervis	66.7	32.5	3.8	2.7	94.2
	Z. capricorni	0.0		17.3	13.6	
Area 2	H. uninervis	2875.3	678.3	1016.4	157.3	64.7
Area 3-1	H. ovalis	2839.2	133.5	155.9	30.6	94.5
Area 3-2	H. ovalis	1445.7	110.4	118.3	22.0	91.8
		Above-ground biomass (g/m^2)				
Area 2	H. uninervis	16.9	4.7	4.6	0.8	73.0
Area 3-2	H. ovalis	22.6	2.2	1.0	0.2	95.8
		Below-ground biomass (g/m^2)				
Area 2	H. uninervis	137.6	13.9	94.8	11.5	31.1
Area 3-2	H. ovalis	27.9	2.5	8.0	1.1	71.3

Table 6.18. Results of analysis of variance of the of the exclosure experiment which examined the response of shoot density ($\log_{10}$ (shoot density + 1) of three species of seagrass under three regimes of simulated grazing by dugongs.

Factor	Error term	df	MS	F	p
Site	Site*Trt	2,4	0.598	1.84	0.2507
Treatment (Trt)	Site*Trt	2,4	5.591	17.23	0.0108
Site*Treatment	–[1]	4	0.324		
Time	Time*Sit	3,6	3.902	7.95	0.0164
Site*Time	–[1]	6	0.491		
Species (Spec)	Spec*Site	2,4	1.366	0.94	0.4631
Site*Species	Site*Spec*Trt	4	1.455		
Treatment*Time	Trt*Time*Site	6,12	1.161	26.61	0.0000
Site*Treatment*Time	–[1]	12	0.044		
Treatment*Species	Trt*Spec*Site	4,8	0.951	1.14	0.4049
Site*Trt*Species	–[1]	8	0.836		
Time*Species	Time*Spec*Site	6,12	0.413	2.23	0.1117
Site*Time*Species	–[1]	12	0.185		
Trt*Time*Species	Trt*Time*Spec*Site	12,24	0.337	6.75	0.0001
Site*Trt*Time*Species	–[1]	24	0.050		
Total		107			

[1] These effects would normally be tested against transects nested within the given effect, however, the error terms are not available as the response was averaged over quadrats and transects.

Table 6.19. Reduction in shoot density (%) of each species of seagrass resulting from simulated grazing at two intensities.

Site	Percentage reduction in shoot density			
	H. spinulosa	H. ovalis	Z. capricorni	Mean
	Low-intensity grazing treatment (along 'feeding trails')			
1	92.4	83.3	91.1	88.9
2	83.7	78.5	90.4	84.2
3	99.2	91.1	92.5	94.3
	High-intensity grazing treatment			
1	84.8	82.1	94.4	87.1
2	83.5	69.4	83.0	78.6
3	76.3	81.1	92.1	83.2

Table 6.20. Incidence of macro-invertebrates in the diet of dugongs. Studies which recorded the absence of invertebrates, or did not refer to their presence have been included only if at least 15 samples were analysed.

Invertebrate	# Samples	Comment	Reference
Crabs	1 stomach	stomach contained 'quantities of marine algae and crabs'.	Hirasaka (1932)
Colonial hydroid	49 stomachs[1]	'a few'	Spain and Heinsohn (1973)
Holothurian		1 specimen	
Ascidian		1 specimen	
Holothurian	6 stomachs	1 in a stomach and 1 in a caecum (35 and 60mm long)	Lipkin (1975)
Hydrozoan		'a few fragments' in 1 gut	
Sponge	3 stomachs 3 faeces	1 specimen	Wake (1975)
Invertebrates	15 stomachs	none recorded	Gohar (1957)
Invertebrates	15 stomachs[1]	none recorded	Heinsohn and Birch (1972)
Invertebrates	102 mouth samples	none mentioned	Johnstone and Hudson (1981)
Invertebrates	95 stomachs[1]	none mentioned	Marsh et al. (1982)

[1] Reanalysis of some of the same material

Figure 6.1. Frequency distribution of grain sizes (mean plus SE) in sediments from 8 'random' sites and 21 feeding sites in the East study area.

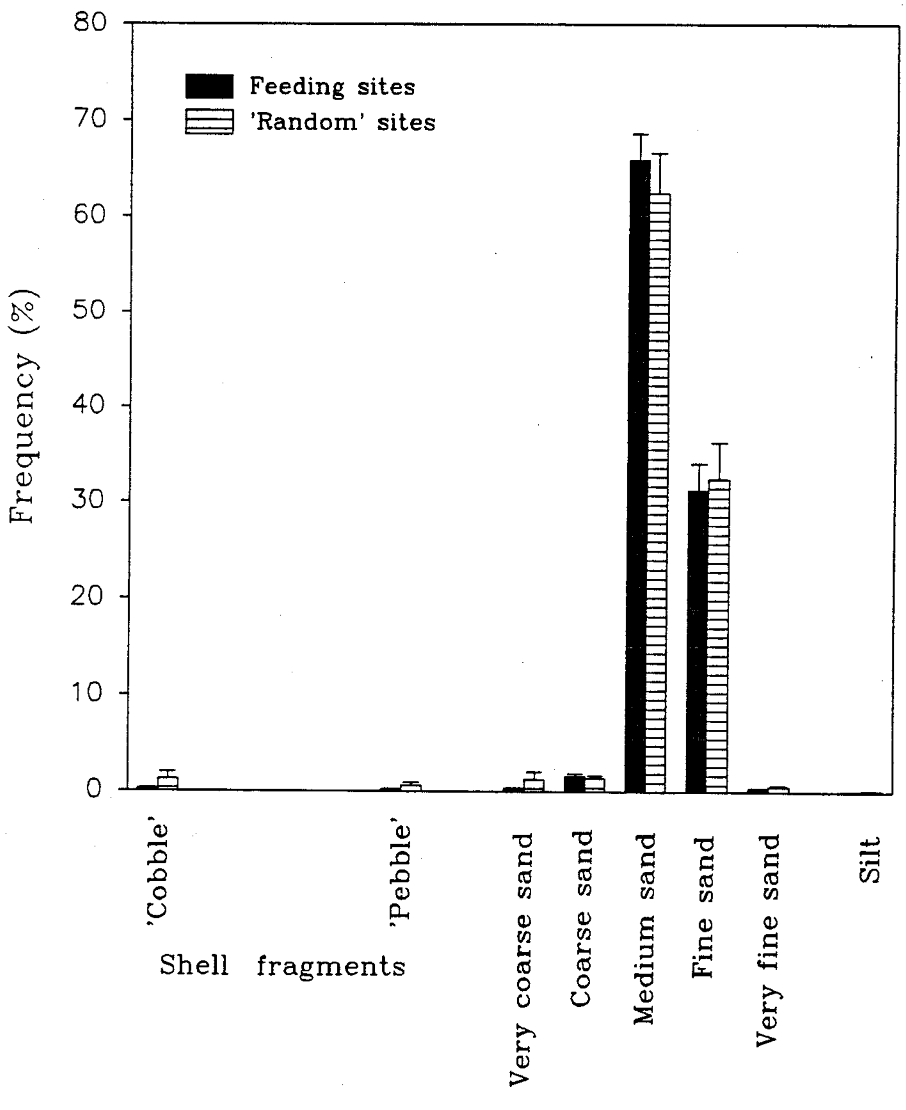


Figure 6.2. Amount of shell and shell fragments (mean plus SE) in surface sediments at 'random' sites and at feeding sites in the study areas. The amount of shell did not differ significantly among feeding sites with the same capital letter. Multiple comparisons were based on the Least Significant Difference.

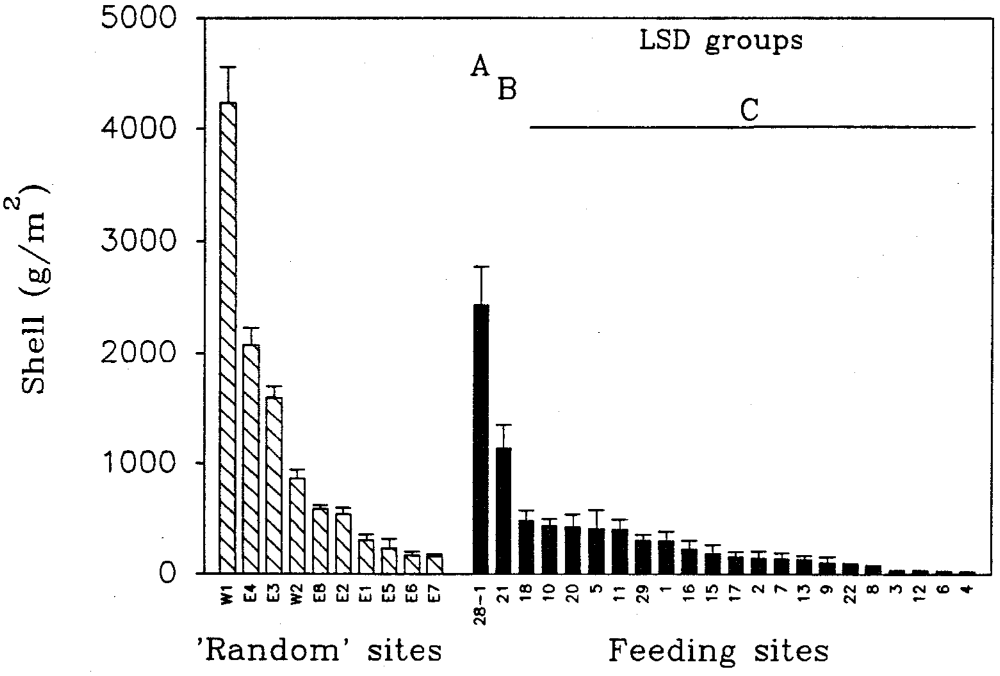


Figure 6.3. Penetrometer readings (mean plus SE) at 'random' sites and at feeding sites in the study areas. Depth of penetration did not differ significantly among feeding sites with the same capital letter. Multiple comparisons were based on the Least Significant Difference.

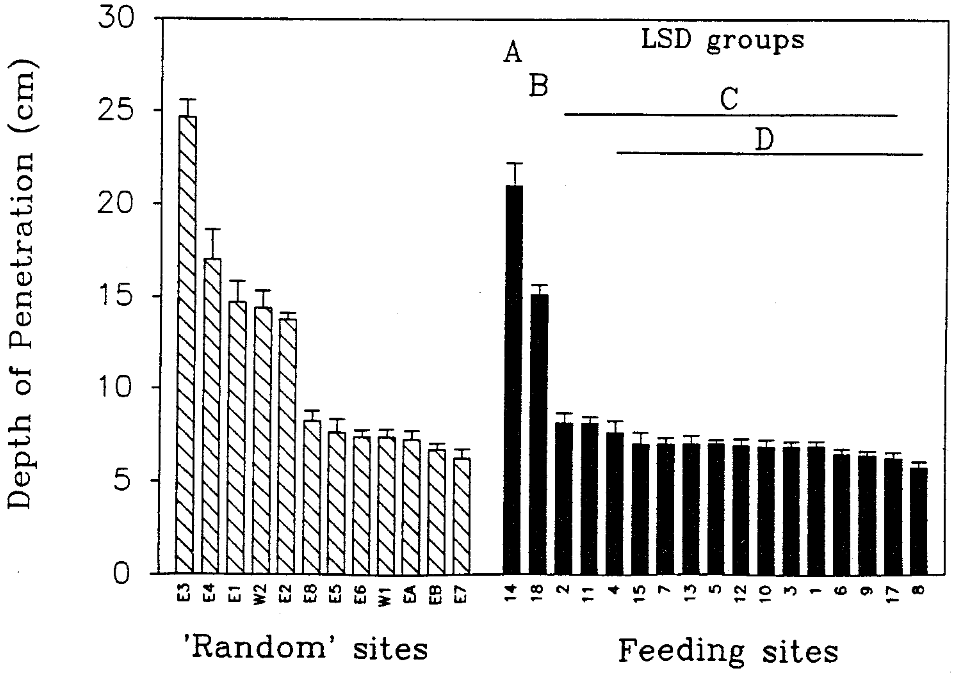


Figure 6.4. Mean (plus SE) abundance of seagrass measured along feeding trails (○) and adjacent to feeding trails (●) at 12 feeding sites. Values are square root transformed. Sites are ordered by decreasing shoot biomass.

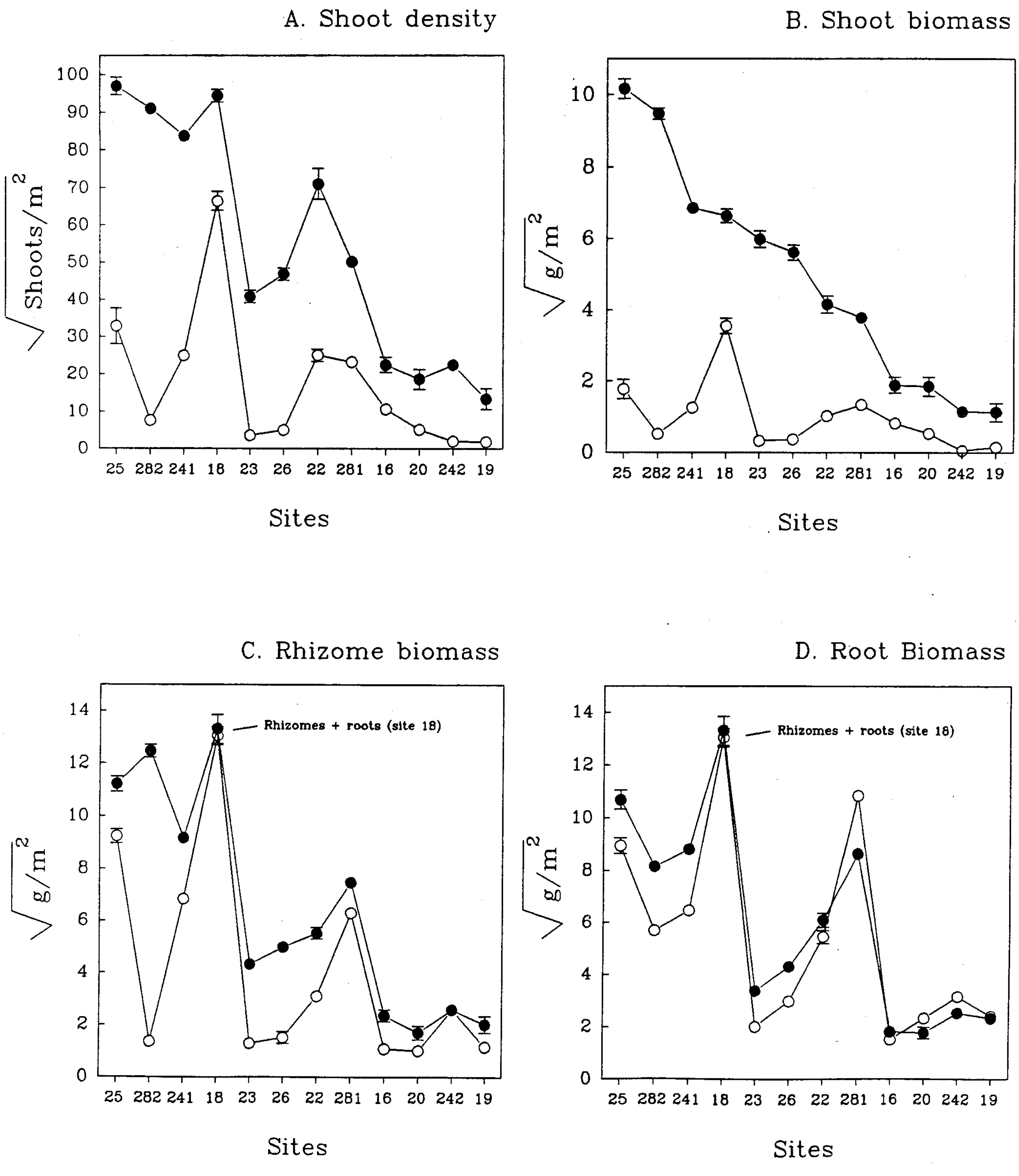


Figure 6.5. Flow chart of steps in the preparation of faecal and stomach samples from dugongs.

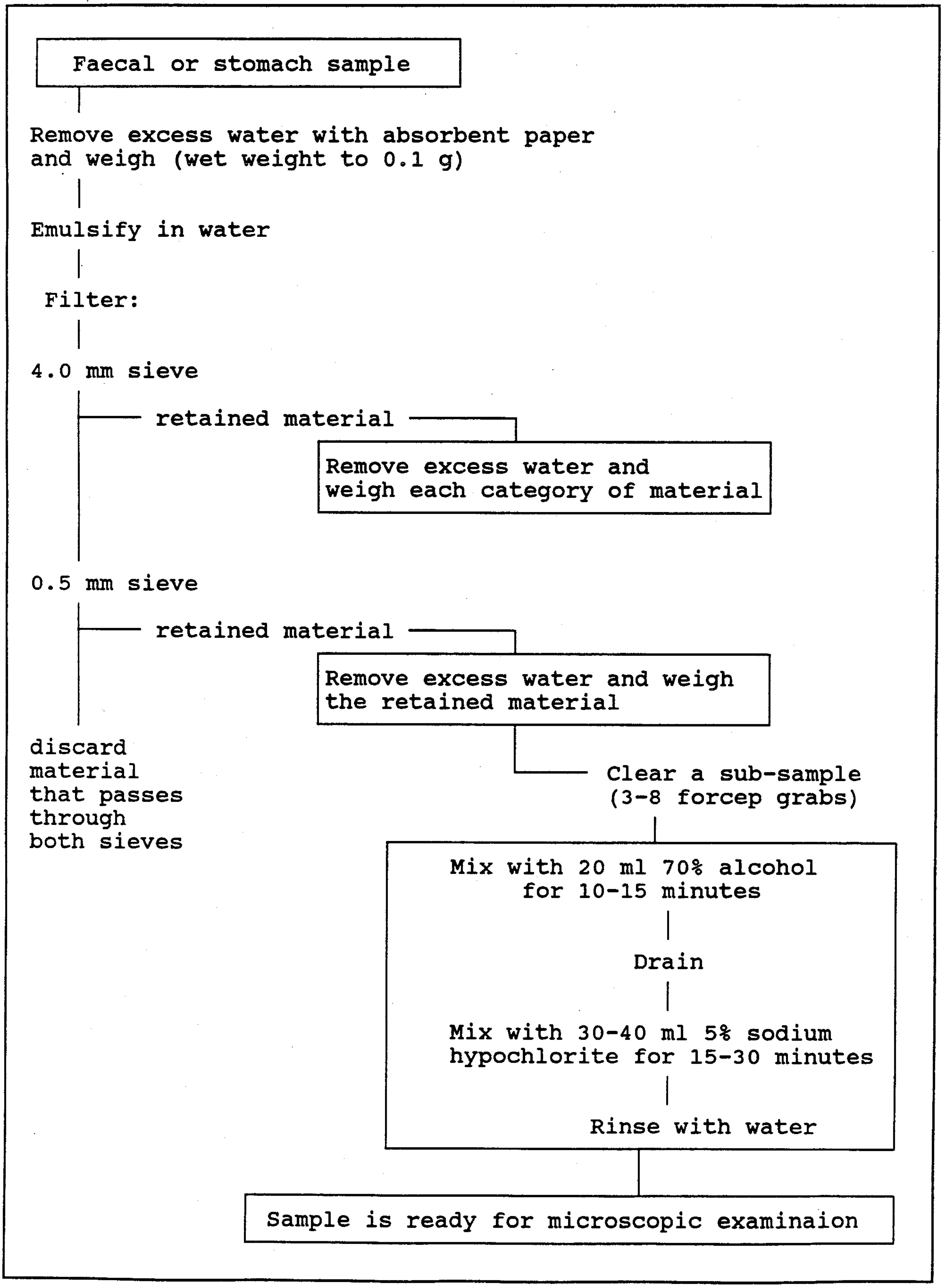


Figure 6.6. Dugong grazing and disturbance of seagrasses. Effects of grazing at Area 3.

A. The ungrazed tract of seagrass, composed of H. ovalis (96% of shoots) and H. uninervis thin (4%). Total shoot density of 2,949 (SE = 139) shoots/m². Shoots of H. ovalis in the picture were 34.5 mm (SE = 3.6) tall.

B. A single dugong trail at the same location.

C. The same location after a few hours of grazing by about 70 dugongs. Dugongs continued to graze this area for 17 days, reducing the density of shoots by 95% over an area of 41 ha.

Figure 6.7. Impacts of intensive grazing by dugongs at Area 2, a meadow of *Halodule uninervis*. ○ □ ◇ refer to transects 1, 2 and 3, respectively. The abundance of seagrass prior to grazing (▲) has been seasonally adjusted to show the expected changes in the absence of grazing. * indicates when grazing ceased.

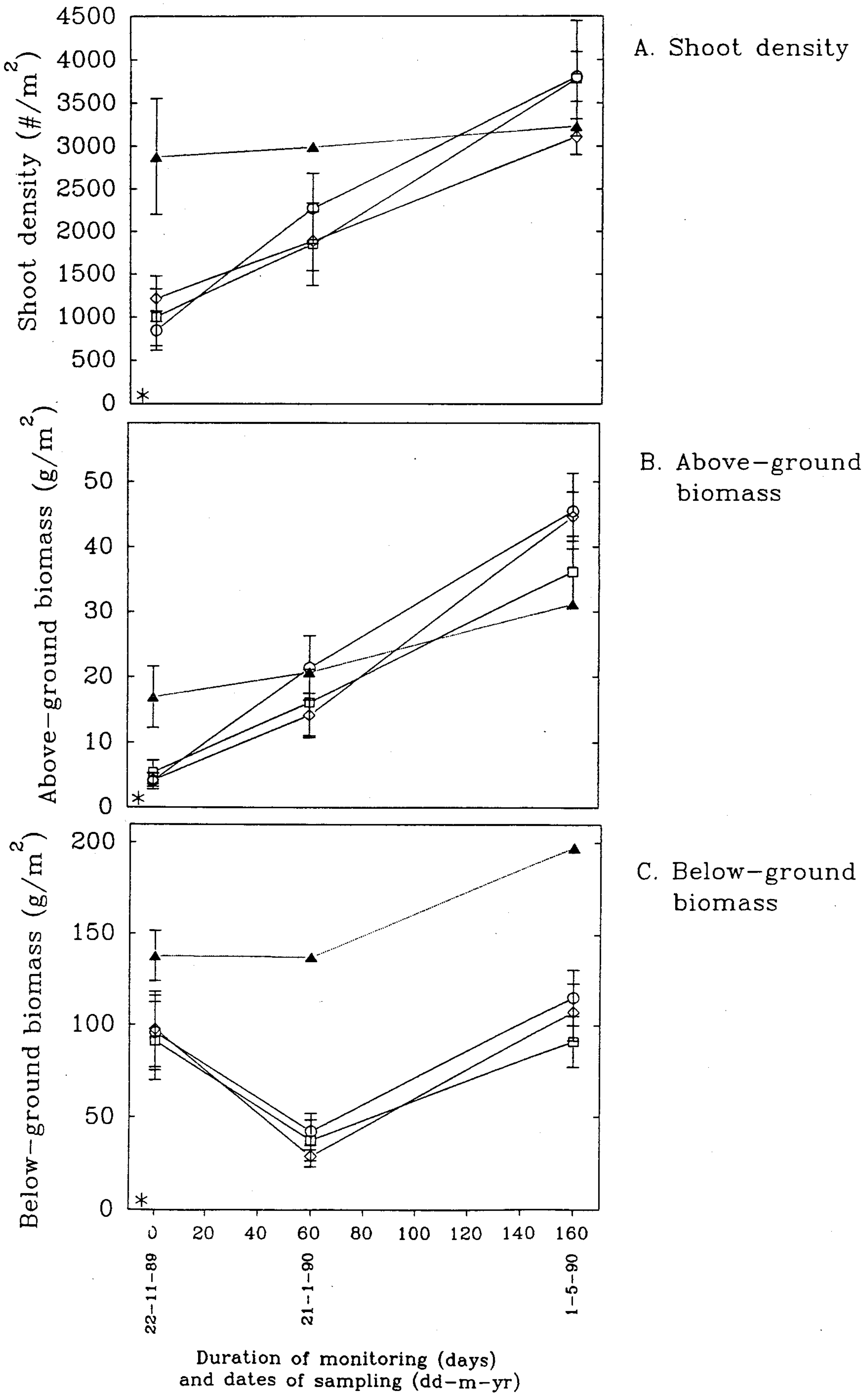
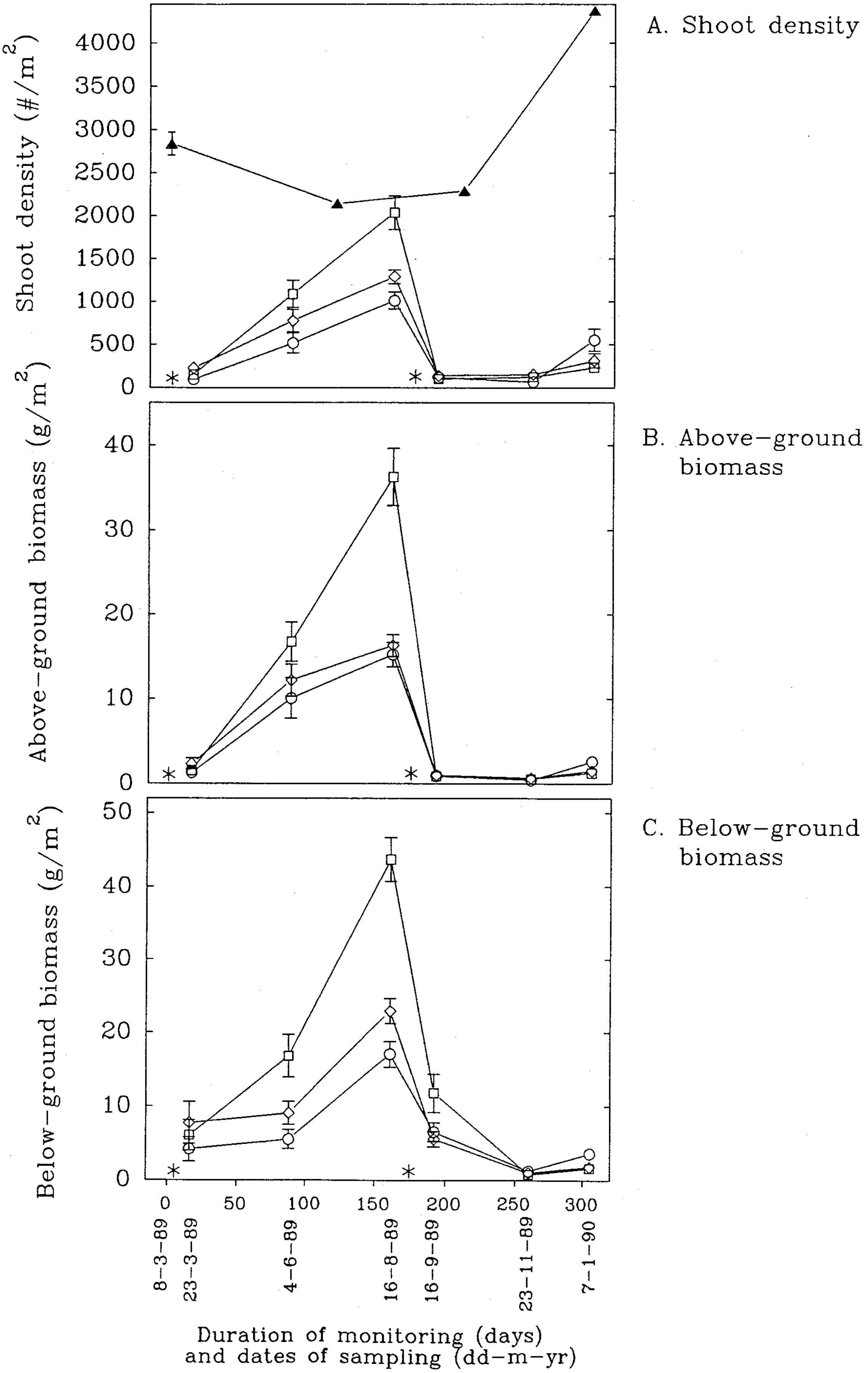


Figure 6.8. Impacts of intensive grazing by dugongs at Area 3, a meadow of *H.ovalis*. ○ □ ◇ represent transects 1,2 and 3, respectively. The density of shoots prior to the first grazing (▲) has been seasonally adjusted to show the expected changes in abundance in the absence of grazing. * indicate the timing of the first and second grazing events.



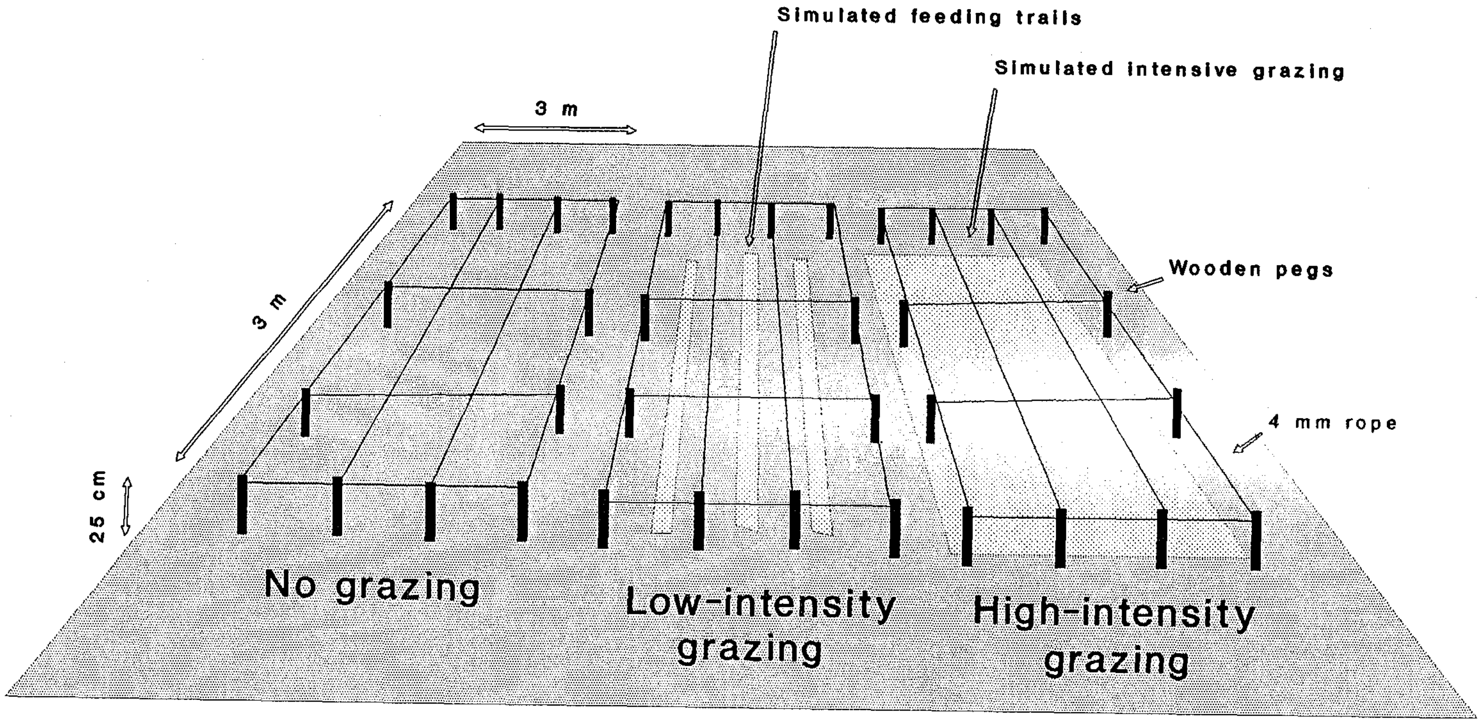


Figure 6.9. Design of exclosures and the set of seagrass treatments established at each of three sites. Treatments were usually several metres apart.

Figure 6.10. Shoot density (mean plus SE) of three species of seagrass in the exclosure and the adjacent unprotected control plot at site 4.

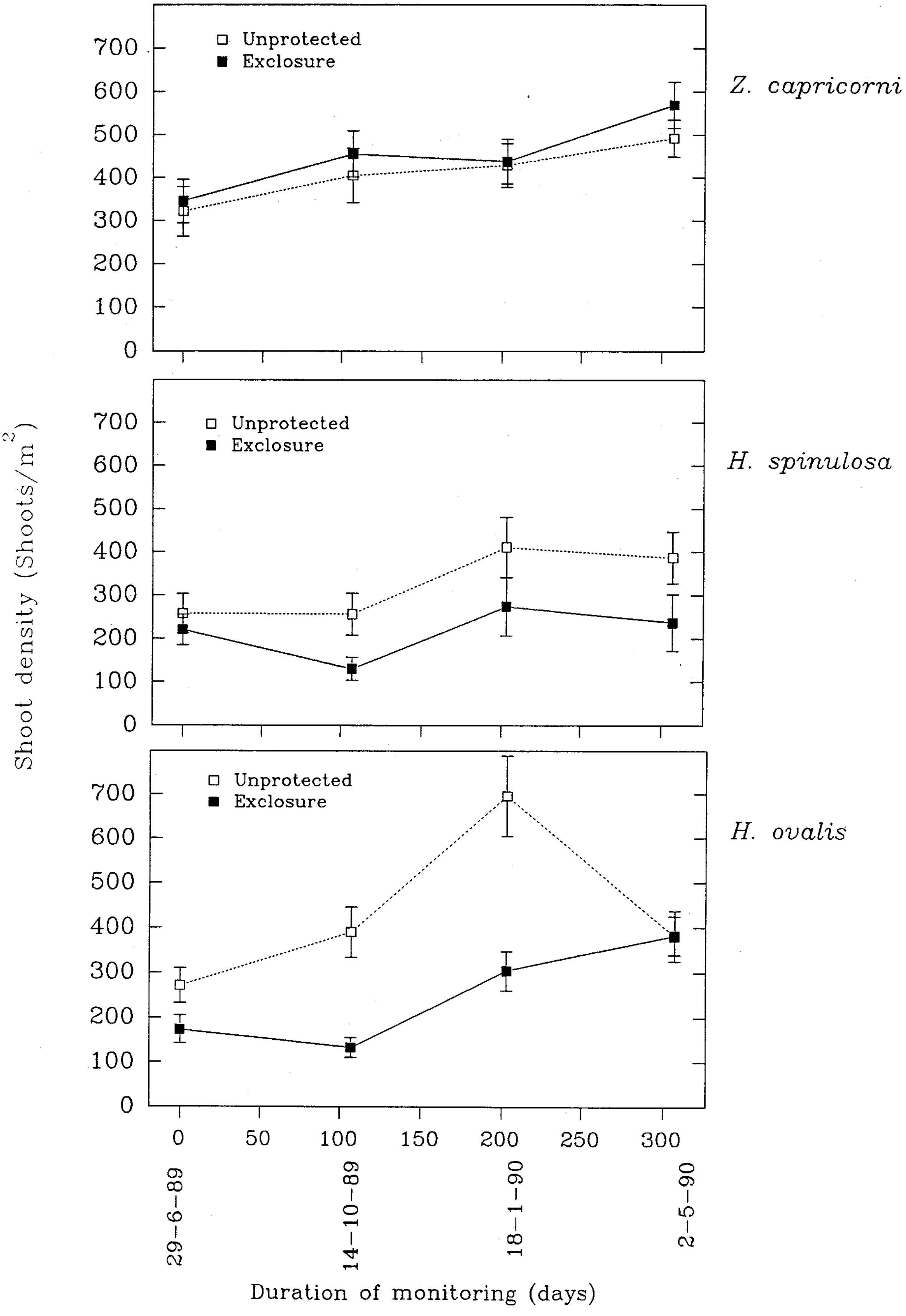


Figure 6.11. Changes in shoot density ($\log_{10}$(shoot density +1)) of three species of seagrass under three treatment regimes. Critical LSD values compare species within times.

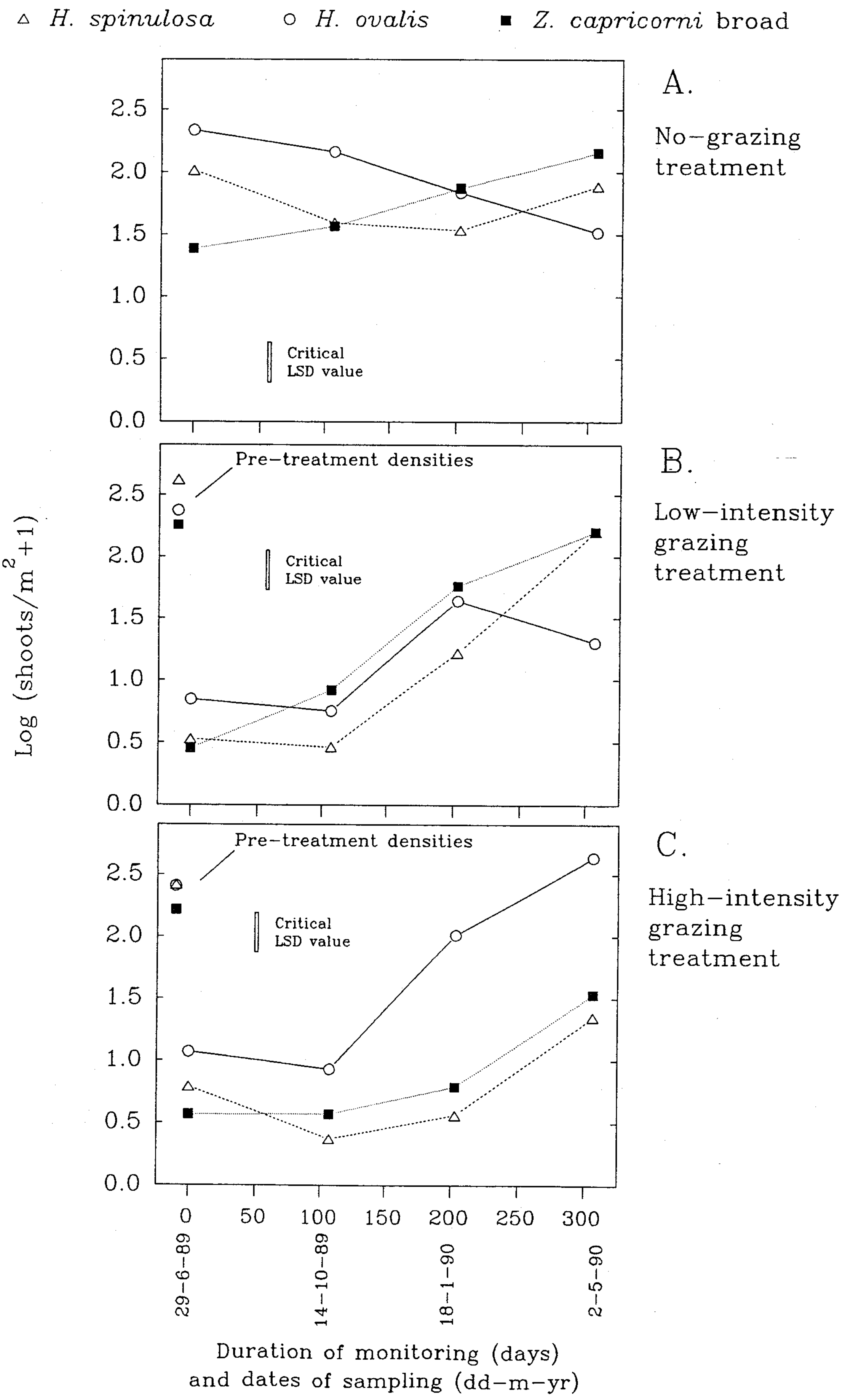


Figure 6.12. Abundance (mean plus SE) of *H. ovalis* (○), *H. spinulosa* (△) and *Z. capricorni* (■) at site E5 over 21 months. This site was probably heavily grazed by dugongs 3–6 months prior to the first sampling.