CHAPTER 8.

ECOLOGICAL SIGNIFICANCE OF LARGE GRAZERS IN THE SEAGRASS SYSTEM

8.1. Grazing as a landscape process

Spatial patterns in natural landscapes result from complex interactions between physical and biological forces (Turner, 1989). Disturbance is one important ecological process that affects temporal and spatial heterogeneity in communities (Sousa, 1984). In concert with previous history and edaphic conditions, disturbance can determine the vegetation mosaic observed at the landscape level (Turner, 1989). Both the intensity and the frequency of disturbance are important factors in this process (Sousa, 1984; Turner, 1989).

In seagrasses, frequent disturbances select for rapidly developing species, while infrequent disturbances provide for a much longer period of community development (Clarke and Kirkman, 1989). 'Cultivation' grazing by dugongs can constitute a major disturbance to seagrass communities and has the potential to alter the species composition of particular seagrass meadows, at least in the short term (1-2 year time frame; Figures 6.11 and 6.12). Could spatial variation in the frequency of 'cultivation' grazing account for some of the spatial heterogeneity of seagrass communities seen in the East study area (Figure 3.1)?

Table 8.1 details four regions of the East study area that were grazed to different extents by dugongs. The Turtle region consisted of the core area of the Turtle Bank. Claire's region contained Claire's Complex, excluding the deep areas that were accessible to dugongs at all tides. The Maroom region was equivalent to the Maroom Bank, excluding some deeper areas at the edges. The Dunwich region contained the southern Warragamba Bank and the Dunwich Bank, excluding some inter-tidal areas, and the area south of Dialba Passage (where oyster leases, fish netting and boat traffic may have deterred grazing dugongs). The depths of each region (Figure 8.1) were significantly different (one-way ANOVA: df = 4, 104; F = 12.10; p = 0.0001). However, each region was within the range of depths

routinely grazed by dugongs (the mean depth of 27 feeding sites was -0.09 m relative to datum).

The total number of dugongs seen on each of these regions during the aerial surveys ranged from 23 to 1,842 (Table 8.1). These counts provide an indication of regional grazing pressure as the surveys were conducted at high tide, when the dugongs had maximum access to the seagrass banks, and because most of these dugongs were probably feeding (based on observations from the aircraft). When these counts are expressed as a percentage of the total number of dugongs seen on seagrass during the surveys, they represent an index of grazing pressure in each region (Table 8.1). Multiplying these indices by the total area of seagrass disturbed annually by the entire dugong population (67.9 km^2; Appendix 7.2) gives a measure of the cumulative area of seagrass disturbed by dugongs each year in each region (Table 8.1). This figure, as a proportion of the area of each region, provides an estimate of the turnover rate: the mean time required for grazing dugongs to disturb the entire area of each region (Sousa, 1984; Table 8.1).

The four regions span a range of feeding-disturbance regimes, with turnover rates ranging from 5 months (Turtle) to 24 years (Dunwich; Table 8.1). The four regions also reflect clear gradients of seagrass composition and abundance, which appear to represent stages in a succession.

Figure 8.2 shows the relationship between the total biomass of seagrass (above- and below-ground parts of all species) and turnover rate ($\log_{10}$ transformed) in the four regions. With more time for community development, infrequently disturbed regions develop a higher biomass of seagrass.

Within the range of depths covered by these regions, Z. capricorni broad, in the absence of grazing disturbance, is the dominant species, forming what is probably a climax community with H. uninervis broad (Figure 8.3). The high biomass and relatively slow growing Z. capricorni broad, however, is apparently unable to survive high rates of disturbance, as it was absent from the two regularly disturbed regions (Turtle and Claire's; Figure 8.3). In those highly disturbed

regions, successional development would be constantly interrupted by grazing. In the most disturbed (Turtle) region only the known pioneer species, H. ovalis and H. uninervis thin (Birch and Birch, 1984; Brouns, 1987b) survive (Figure 8.3).

H. spinulosa appears to prefer moderately high rates of disturbance, as it was absent from the most disturbed and least disturbed regions (Figure 8.3). Although H. spinulosa occurred only in the deeper regions, the mean depths of Claire's region (where it occurred) and the Dunwich region (where it was absent) were not significantly different (Least Significant Difference comparison; Figure 8.1), suggesting that depth is not the only factor determining the distribution of H. spinulosa in these four regions. It is unlikely that the regional variation in the abundance of H. ovalis and Z. capricorni broad is attributable to water depth, as the depths of the Turtle and Dunwich regions, at each extreme of the successional series, were not significantly different (Least Significant Difference comparison; Figure 8.1).

The estimates of turnover rate in each of the regions are based on some crudely measured parameters (feeding rate, feeding efficiency and population size; Appendix 7), and may not be correct in an absolute sense. However, their relative values should be correct, as the regional measures of grazing pressure were independent of the estimates of the actual areas disturbed.

The correlative relationship between the rate of grazing disturbance and the relative abundance of each species of seagrass may be an example of pattern influencing process (see Turner, 1989): the dugongs prefer to feed in some areas, or choose to avoid others, because of the seagrasses that are there. This is doubtlessly occurring, however, the exclosure experiment demonstrated that the intensive grazing by dugongs can also change the relative abundance of seagrasses by favouring H. ovalis, their preferred species, and retarding Z. capricorni broad. Direct evidence that dugong grazing is responsible for the maintenance of the observed regional differences in seagrass composition is lacking. An attempt to demonstrate this role of dugong grazing, using exclosures in the Turtle region, was unsuccessful. By providing shelter, the exclosures allowed seagrass-eating fish (particularly Monocanthus chinensis) to establish territories in the otherwise

shelterless expanse, resulting in increased grazing inside the exclosures.

The Maroom region, which had an intermediate turnover rate, contained the highest number of seagrass species. H. ovalis, H. spinulosa and Z. capricorni broad all occurred in this region at relatively similar biomasses (7.3, 15.5 and 36.3 g/m² respectively). In the other regions, especially the most or least disturbed regions, one species tended strongly to dominate (Figure 8.3). These data are consistent with the intermediate disturbance hypothesis of Connell (1978) which predicts that species diversity will be greatest in communities experiencing an intermediate frequency of disturbance. Under such a regime of disturbance, competitively dominant species are prevented from monopolising resources. Relative species diversity has been accounted for by intermediate rates of disturbance in a wide variety of communities (Connell, 1978; Hemphill and Cooper, 1983; Hinds and Ballantine, 1987; Sousa, 1979).

The diversity of species of seagrasses outside the depth range of these four regions is not accounted for by grazing disturbance. Most of the shallower areas are rarely grazed by dugongs, and in inter-tidal areas and deep water areas, other constraints, such as exposure or light attenuation may be more important in determining the composition of species.

8.2. Grazing and energy flow in seagrass systems

Only a small proportion of the production of seagrass beds is consumed directly by grazers in almost all systems so far studied. Consequently, energy flow within seagrass systems is believed to be dominated by decomposition processes (Kirkman and Reid, 1979; Klumpp et al., 1989; Poiner et al., 1992; Thayer et al., 1984). Direct consumption of above-ground seagrass production amounts to 5-10% (fish and urchins) in the Caribbean (Zieman et al., 1979), <5% (by fish) in the northern Red Sea (Wahbeh, 1980 cited in Sheppard et al., 1992), 3% (fish and amphipods) in south-eastern Australia (Kirkman and Reid, 1979), 4-8% in northern Europe (Nienhuis and Groenendijk, 1986) and <3% (waterfowl) in north America (Thayer et al., 1984).

Sea urchins provide the only documented exceptions to this pattern of minimal direct grazing. In the northern Red Sea, the urchin Tripneustes gratilla occurred at a density of about $1/m^2$, and consumed about one third of the above-ground production of H. stipulacea (Wahbeh, 1980 cited in Sheppard et al., 1992). In Kingston Harbour, Jamaica, the urchin Lytechinus variegatus, at an atypically high density (Ogden, 1980) of $20/m^2$ consumed 48.1% of the production of a T. testudinum meadow (Greenway, 1976). High densities of urchins, and associated atypical levels of grazing, result from over-harvesting of reef fish populations (Hay, 1984).

No data have been available on the amount of seagrass production consumed by large grazers, such as sirenians and green turtles. Several authors have noted, however, that the trophic relationships within some seagrass systems may have altered in historical times, as a result of the dramatic reduction in the abundance of these consumers (Bjorndal, 1980; Hay, 1984; Thayer et al., 1984). Prior to the arrival of Europeans, populations of green turtles in the Caribbean were orders of magnitude greater than today (Bjorndal, 1980). For instance, many of the rookeries described as good turtling beaches in the logs of 16th- and 17th-century ship's captains, some of which yielded harvests of 1,000-2,000 turtles per *night* are no longer used by turtles (Bjorndal, 1979, 1980). Likewise, populations of dugongs and manatees are believed to have been greatly reduced in many areas (Bertram and Bertram, 1973; Caldwell and Caldwell, 1985; Lefebvre et al., 1989; Thornback and Jenkins, 1982).

Although it is unknown what impact the disappearance of these large herbivores has had on seagrass systems, Bjorndal (1980) and Hay (1984) have cautioned against extracting evolutionary implications about seagrass systems from ecological data in the absence of such 'missing species'. This Moreton Bay study has provided a valuable opportunity to assess the ecological significance of one of the few large consumers of seagrass, the dugong, in a relatively undisturbed system.

At the scale of the East study area (110 km^2 of seagrass), dugongs consume only about 1% of the annual above-ground production of seagrass (assuming: [1] a

population of 600 dugongs (section 5.4.1), [2] annual above-ground production of 34,399 tonnes DW seagrass (Table 4.12) and [3] daily consumption of 3.22 kg DW seagrass/dugong (Appendix 7.1) of which about half would be above-ground components). However, this is an inappropriate spatial scale, as the distribution of dugongs in was very uneven: many high-biomass areas, with consequently high production, were not used by the dugongs (section 5.4.4).

Consideration of a more appropriate scale results in a different perception of the ecological significance of dugong grazing. In the core area of the Turtle Bank (5.65 km²), where grazing pressure is high (Table 8.1) I estimate that the dugongs consume 28% of the annual above-ground production of seagrass (Appendix 8). If total production (above- plus below-ground) is considered, the proportion consumed by dugongs remains at approximately 28% (below-ground production of H. ovalis is 50% of total production [Hillman et al., 1989] and 50.4% of consumption by dugongs feeding on H. ovalis is made up of below-ground material; Appendix 8.2.4). By contrast, other grazers (cited above) consume only above-ground material, so in terms of the proportion of total production consumed, their significance is even less than indicated (below-ground production accounts for 10-50% of total production in most species; Hillman et al, 1989).

It is clear that in favoured areas, dugongs can have a substantial influence on energy flow within seagrass systems. As described in section 6.6.3, this level of consumption may have a profound influence on the biomass and species composition of seagrass communities.

Extrapolation of this conclusion, to a generalisation, is fraught with problems. There are no comparative data on the distribution and density of dugongs from other areas, that has been collected at an appropriate scale. How typical the grazing pressure on the Turtle Bank is, therefore, cannot be judged at this stage. Furthermore, dugongs in other areas are not known to concentrate their grazing in the manner that has been described for Moreton Bay dugongs ('cultivation grazing'; section 7.7.4). Consequently, in other areas, a lower percentage of seagrass production may be consumed within a given area.

Manatees are not known to feed in herds, except near warm-water refuges, although their grazing behaviour may have differed when they were more abundant (see section 7.4.5.4).

When assessing the ecological role of green turtles in the seagrass system, relative to dugongs, a number of differences must be considered. Firstly, not all green turtles feed on seagrass (Bjorndal, 1980, 1985; Lanyon et al., 1989), although those in inshore bays and estuaries (where seagrass is most abundant) usually do (Lanyon et al., 1989). When feeding on seagrasses, green turtles generally consume only the leaves (Bjorndal, 1979; Lanyon et al., 1989), whereas dugongs feed on the leaves, rhizomes and roots (section 6.6.1.2). The impact of grazing by turtles, therefore, is likely to be less than that of dugongs (Thayer et al., 1984). Individual green turtles also consume much less seagrass than dugongs. Because they are poikilotherms, with correspondingly low metabolic rates, green turtles consume the equivalent of only 0.6-2.2% of their body weight daily (Bjorndal, 1980; Fenchel et al., 1979; Thayer et al., 1982). This compares with 7.1-15.7% for manatees (depending on age and reproductive condition; Best, 1981; Etheridge et al., 1985). Adult green turtles (64-170 kg) consume 80-120 kg dry weight seagrass/year (Bjorndal, 1979; Fenchel et al., 1979; Thayer et al., 1982). This is an order of magnitude less than an adult dugong (1,175 kg dry weight/year; Appendix 7.1). However, compensating for this difference, turtles are probably at least an order of magnitude more abundant than dugongs in areas where there is relatively low hunting pressure (eg. in northern Australian waters; H. Marsh, pers. comm.).

Acknowledging the problems of extrapolating beyond Moreton Bay, and the ecological differences between dugongs and green turtles, it is apparent that in areas where both species are abundant, the proportion of seagrass production passed through grazer pathways may be substantially greater than previously recognised. This conclusion contrasts with widely stated generalisation that energy flow within seagrass systems are based on detritus (Kenworthy et al., 1988; Kirkman and Reid, 1979; Klumpp et al., 1989; Poiner et al., 1992; Thayer et al., 1984; Zieman and Wetzel, 1980). All previous studies have been conducted in the absence of large herbivores.

Grazing by dugongs (and possibly turtles), in areas where they are abundant, could affect the community ecology of the seagrass ecosystem. Fish and invertebrate assemblages have been shown to change with changes in the physical complexity of seagrass meadows (Orth and Heck, 1980), which may be due to different levels of protection provided by the seagrasses (Heck and Orth, 1980). For example, Stoner (1983) found a significant positive correlation between the abundance of fish and the density of seagrass leaves (but not leaf biomass) across three species of seagrass, and the survival of invertebrate prey can be enhanced when the surface area or density of seagrasses is increased (Bell and Pollard, 1989 and references therein). Persistent grazing by dugong herds may change the physical structure of seagrass beds (from high to low biomass and late to early seral-stage; section 6.6.3) and thereby alter the assemblages of fish and invertebrates.

When a significant proportion of seagrass productivity is consumed by large herbivores, such as green turtles or dugongs, the populations of detritus feeding organisms may also be affected. Green turtles return a partly digested faecal product to the system that has a higher C:N nutritional quality than the seagrass. Turtles feeding on T. testudinum in the Caribbean produced a daily average of 2.9 g nitrogen as faecal material, compared with an estimated daily release of 0.04 g nitrogen from the decomposition of the equivalent amount of seagrass (Thayer et al., 1982). Thus by increasing the rate of nutrient turnover, turtle (and presumably dugong) grazing may enhance the populations of detritus feeding organisms, and therefore, secondary productivity.

However, when dugongs and turtles move off the seagrass banks, the contents of faecal material will be lost from the seagrass system. In Moreton Bay, dugongs spend substantial periods outside the Bay during winter, and rarely defecate on the seagrass banks during this season. Breeding green turtles, which migrate to other areas to nest, also export substantial quantities of nutrients, in the form of eggs, from the seagrass system (Lanyon et al., 1989).

8.3. Competition between dugongs and green turtles

Wherever they coexist, dugongs and green turtles probably share the same seagrass resource. The extent to which they partition this and other food resources has not been examined.

In some areas where both dugongs and green turtles occur, at least some turtles feed predominantly on algae (Garnett et al., 1985; Lanyon et al., 1989; Nietschmann, 1984). In other areas, the two species may feed primarily on different seagrasses, although the evidence is scant (some turtle- and dugong-hunting Aborigines have different names for seagrasses that are apparently eaten by only turtles or dugongs; Bradley, 1991).

On the Moreton Banks in the East study area in Moreton Bay, both dugongs and green turtles feed on the same seagrasses (Read, 1991; section 6.4.1.2). The dugongs feed primarily on species of Halophila, as well as H. uninervis, Z. capricorni, S. isoetifolium and ascidians. Insignificant quantities of algae were detected in the faecal samples (sections 6.4.1.2 and 6.6.2). By contrast, green turtles in Moreton Bay feed on algae as well as seagrasses and some animals. The most important species in the crop samples lavaged from 269 green turtles captured on the Moreton Banks were the seagrass H. ovalis (>50% volume of 17% of samples) and the red algae Hypnea cervicornis and Gracilaria edulis (>50% volume of 20% of samples; Read, 1991). As well as other seagrasses and algae, they also consumed mangrove seeds and animals (cnidarians and molluscs: different phyla to those exploited by the dugongs; Read, 1991).

While the dugongs fed selectively at a variety of scales (section 6.6.3), there was little evidence to suggest that the turtles fed selectively on seagrasses. The stomach-flushing technique samples fresh ingesta from the crop region (Read, 1991), and the relative abundance of seagrasses in the lavage samples from different areas on the banks was in accord with the distribution of species in those areas. (It should be noted that Read [1991] interpreted his results to suggest that the turtles were feeding selectively, however, his sampling of seagrass at the point of capture was inadequate, and he had little information on the distribution

of seagrasses).

As previously mentioned, dugongs and turtles also feed on different, but overlapping parts of the seagrass plants. Dugongs feed on the leaves, rhizomes and roots of seagrasses (section 6.6.1.2), while green turtles usually feed only on the leaves (Bjorndal, 1979, 1980, 1985; Lanyon et al., 1989; Read, 1991; Thayer et al., 1982).

While there is broad overlap in the diets of the dugongs and green turtles in Moreton Bay, there are also substantial differences in the composition of their diets. It is unlikely that there is any significant competition for food between coexisting dugongs and green turtles. In fact, the green turtles that feed on the eastern banks in Moreton Bay probably benefit from grazing the same areas as the dugongs. By their 'cultivation' grazing, the dugongs may maintain large areas of seagrass in a nutritionally superior state (relatively high nitrogen and low fibre content; section 6.6.3.4). In the Caribbean, individual green turtles maintain small grazing patches in the seagrass beds, where they regularly crop the new, low fibre, high nitrogen leaves (Bjorndal, 1980; Ogden et al., 1980). In Moreton Bay I never detected any of this type of grazing patch, but the green turtles were most abundant on the Turtle Bank, which may be viewed as an extreme form of a dugong grazing patch.

Table 8.1. Dugong grazing pressure, area of seagrass disturbed and turnover rate of seagrass resulting from grazing in four regions of the seagrass banks in the East study area in Moreton Bay.

Region	Area (km^2)	# dugongs seen during aerial surveys	Percentage of total number of dugongs seen[1]	Area disturbed annually by dugongs (km^2)[2]	Disturbed area as % of total area	Turnover rate[3]
Turtle	5.65	1692	19.90	13.51	239.11	5.0 months
Claire's	4.20	915	10.76	7.31	173.95	6.9 months
Maroom	16.77	1842	21.66	14.71	87.70	1.14 years
Dunwich	4.37	23	0.27	0.18	4.20	23.80 years

[1] Total of 8,504 dugongs seen on areas with seagrass

[2] Based on daily consumption of 28.5 kg wet weight seagrass day^{-1} dugong^{-1} and feeding efficiency of 65.2% and average biomass of 12.3 g DW/m^2 (see Appendix 7)

[3] Average time required to disturb the whole area (1/(area disturbed/area of region)).

Figure 8.1. Mean depth (plus SE) at four regions in the East study area that were grazed to different extents by dugongs (Turtle: very regularly grazed to Dunwich: rarely grazed).
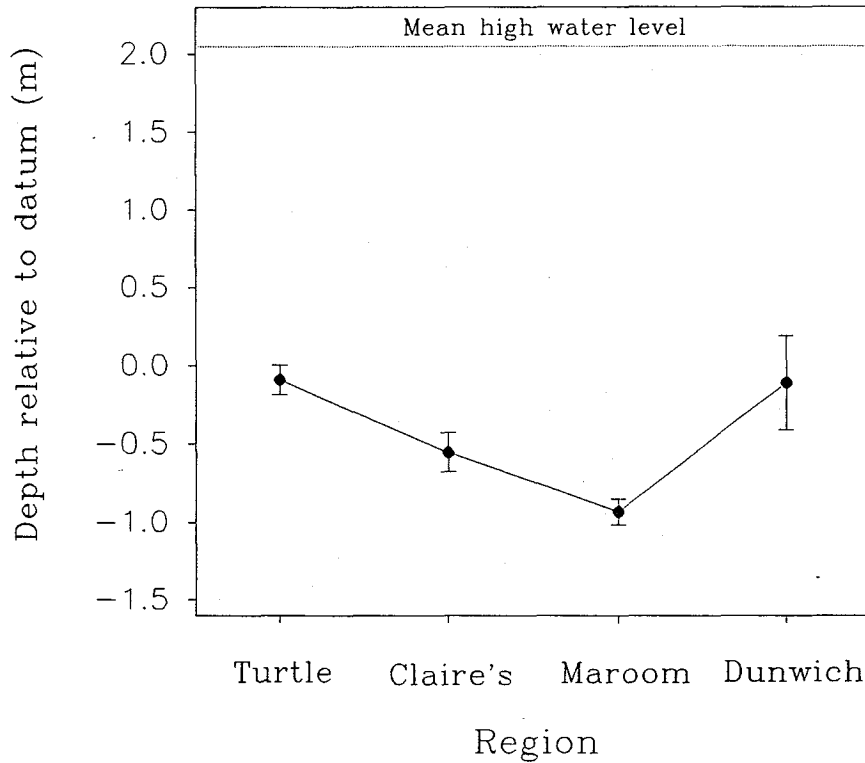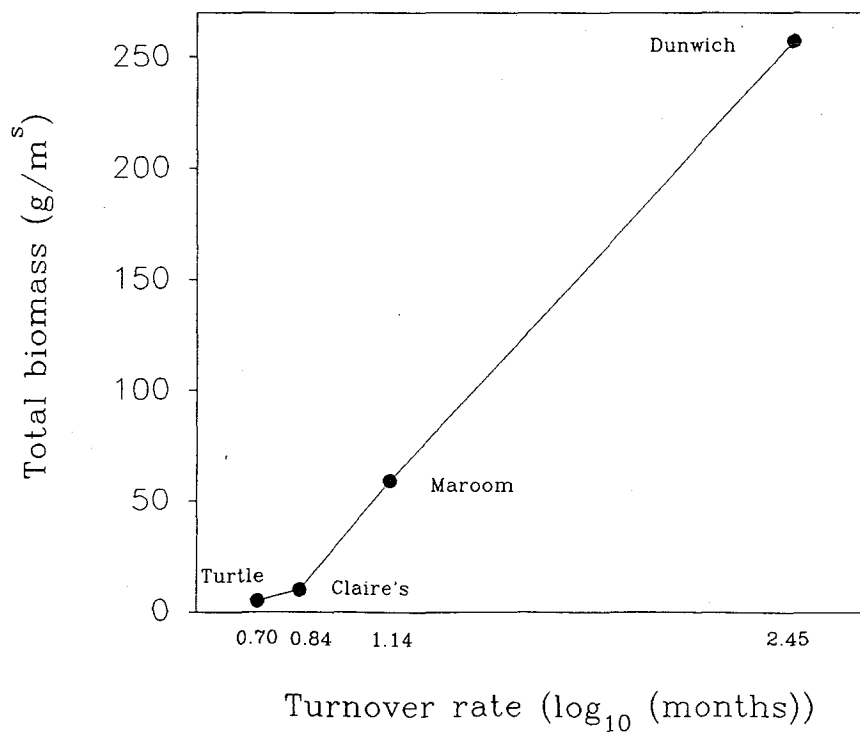

Figure 8.2. Relationship between turnover rate of seagrass due to dugong grazing and total biomass (above− plus below−ground parts) of seagrass at four regions in Moreton Bay.
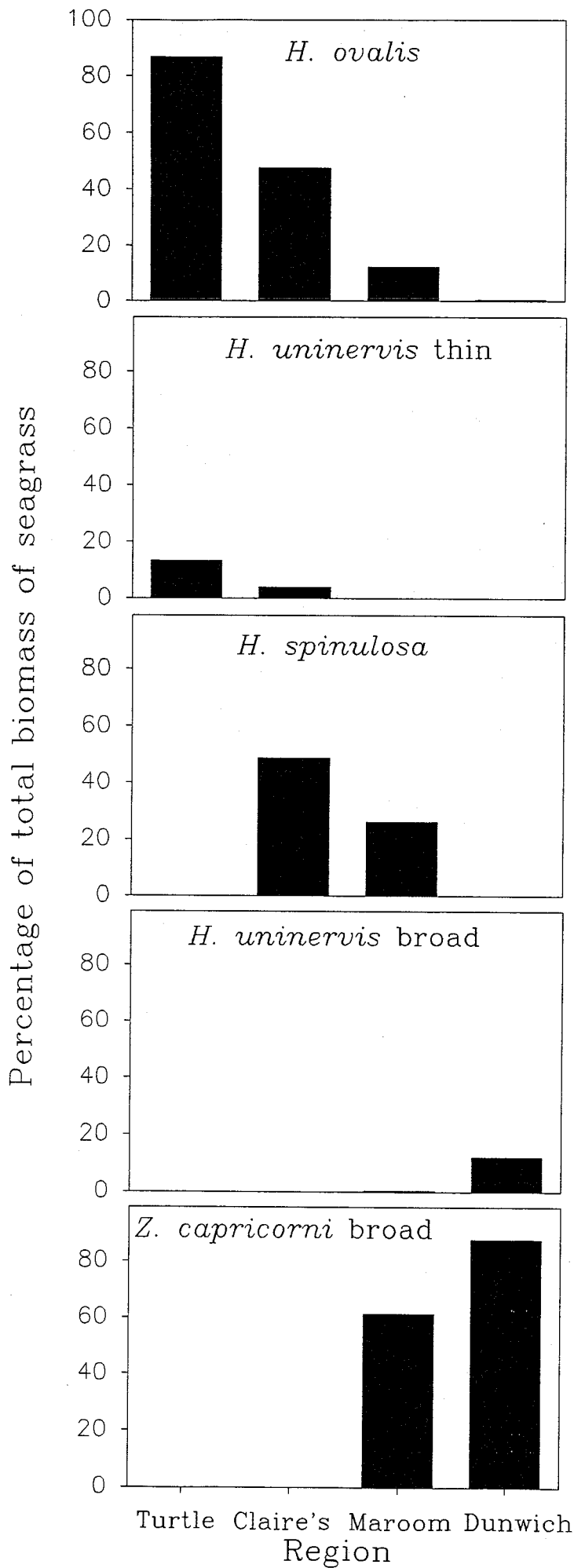
Figure 8.3. Relative abundance of seagrasses in four regions in the East study area that were grazed to different extents by dugongs. Regions are arranged by frequency of grazing, from very frequent (Turtle) to rare (Dunwich).