CHAPTER 4.

TEMPORAL PATTERNS IN THE SEAGRASSES

4.1. Introduction

Seasonal changes in an animal's food supply can have a significant influence on aspects of its life history. In dugongs, patterns of growth and breeding may be determined by the availability of seagrasses (Lanyon, 1991).

The climate of Moreton Bay has pronounced seasons (section 2.2), so substantial changes in the abundance of seagrasses may be expected (Hillman et al., 1989). The quantification of seasonal changes, therefore, is a necessary corollary to the description of spatial patterns (Chapter 3), if the availability of the dugongs' principal food is to be appreciated. The quantification of any seasonal variation in seagrass abundance was the aim of this chapter.

4.2. Methods

Temporal changes in the abundance of five species of seagrass, plus epiphytic and macro-algae, were monitored at 10 sub-tidal sites over two years. Eight of the sites were located in the East study area and two in the West.

The general location of sites was chosen to ensure coverage of a range of seagrass communities. The precise location of each site was randomly determined by the simultaneous alignment of at least two topographic features in at least two directions (to facilitate relocation). To avoid confounding effects resulting from non-climatic variables (depth-related light attenuation, currents, emersion), no sites were located in channels or in inter-tidal areas. Characteristics of the sampling sites are summarised in Table 4.1. In the East study area, two sites were located on each of the following banks: Dunwich (sites E1 and E2), Coonungai (E3, E4), Maroom (E5, E6) and Turtle (E7, E8; Figure 2.2). In the West, site W1 was located near the Darcy Light and site W2 was at the mouth of Tingalpa Creek.

4.2.1. Sample collection

Seagrasses were sampled four times each year for two years. The sampling months (July, October, January and April) corresponded with the winter, spring, summer and autumn seasons, as defined by water temperature (section 2.2.3). Sampling commenced in July 1988 and ended in April 1990. Due to logistical constraints, not all sites were sampled during the first sampling period, nor in the latter sampling periods (Table 4.1).

Samples were collected at 2 m intervals along a 50 m permanent transect at each site. A total of 25 quadrats were destructively sampled per site per sampling period. A pilot study indicated that a 0.05 m² quadrat resulted in the least variance in shoot densities and biomass, for moderate to high seagrass abundances. Sites with a very low density of shoots (site E7: sampling periods 2, 3, 4, 5 and 6; site E8: sampling periods 2, 3 and 6) were sampled with a 0.1 m² quadrat. Quadrats were excavated to a depth of 6-12 cm, depending on the depth of the root and rhizome layer.

Several precautions were taken to avoid re-sampling the same quadrat during subsequent periods. The transect end pegs were 51 m apart and the 50 m transect (with a 1 m end rope) was run-out from alternate ends each sampling period. Quadrats were sampled from alternate sides (east or west) of the north-south oriented transect each sampling period. Additionally, the transect bowed, either to the east or west, between the end pegs. The direction and extent of this distortion depended on the strength and direction of the current and the path swum when the transect was laid out. These sources of variation resulted in each quadrat being haphazardly sampled from an area of approximately 2 m² (range 0.5 - 6 m²) at each sampling period. The impacts of the previous sampling were never apparent.

4.2.2. Treatment of samples

In the laboratory, samples were thoroughly washed in fresh water. There was generally little contamination by encrusting epiphytes or sediment, so acid-treatment (Poiner et al., 1987) was not necessary. When they were present in

measurable quantities, epiphytic algae were scraped from the leaves and treated as a separate category.

The samples were sorted into species of seagrass and the number of shoots counted. New shoots were counted only if the leaf scales had parted. The lengths of about 30 leaves were measured for each species per site per sampling period. To avoid bias, all leaves or leaf clusters were measured on haphazardly selected sections of rhizome. In species with several leaves per cluster (Halodule uninervis, Cymodocea serrulata, Syringodium isoetifolium and Zostera capricorni), the shortest and longest leaves in each cluster were measured. In Halophila ovalis, which has two leaves per cluster, the longest and shortest leaves were measured alternatively.

The samples were separated into above- and below-ground components. The most repeatable demarcation for this separation was the junction of the shoot and the rhizome. The so-called above-ground component, therefore, included all leaf and associated material, such as sheaths and leaf bases which may have been located below the sediment surface. The below-ground component was comprised solely of rhizomes and roots, and I refer to them collectively as rhizome. Total biomass refers to above- plus below-ground biomass. Macro-algae were not separated into above- and below-ground components.

Due to the abundance of dead rhizomes of Z. capricorni, dead rhizome was measured as a separate category. Separation of live and dead rhizomes of Z. capricorni was particularly difficult because of their similar appearance and because they were physically tangled together in the same root and rhizome mat. Unless stated otherwise, the terms below-ground biomass and rhizome, refer to live material. However, as not all of the dead material could always be removed, the values of below-ground biomass for Z. capricorni are slightly biased.

Biomass determinations (g/m^2) were made after samples were oven-dried at 60-65°C to a constant weight. The wet weight of samples was recorded for seagrass collected during the first sampling period only. The relationships between wet and dry weight of above- and below-ground components of the most abundant species

are presented in Appendix 3.

Shoot lengths were recorded for sampling periods 3, 4, 5, and 6 (as defined in Table 4.1). Dead rhizome was recorded during sampling periods 4, 5 and 6. The abundance of macro- and epiphytic algae was recorded during sampling periods 2 to 8, inclusive.

Although two morphs of H. uninervis occurred in samples, the thin-leafed morph was present in only very small amounts (0.20-0.26 g/m^2 at sites E7 and E8), and hence has not been distinguished from the abundant broad-leafed morph. Only the broad-leafed morph of Z. capricorni occurred at the sampling sites.

4.2.3. Correlations with climatic variables

The abundance of seagrass at each site, during each of the eight sampling periods, was tested for correlation with a series of climatic variables which describe the seasonal environment of Moreton Bay. Each site was examined separately, as the differences in seagrass abundance between sites may have obscured relationships with the climatic variables. The dependent variable was the total abundance of seagrass (all species combined) in each quadrat. Separate analyses were conducted for shoot density, above-ground biomass and below-ground biomass. The independent variables were:

1. Water temperature: mean water temperature during the month of sampling.
2. Mean water temperature: mean water temperature during the preceding three months (including the month of sampling).
3. Day length: day length during the month of sampling.
4. Mean day length: mean day length during the preceding three months.
5. Mean rain: average monthly rainfall during the preceding three months.
6. Cloud: the effect of cloud cover on the level of irradiance during the month of sampling. Calculated as

$$Day\ length - (\frac{cloud\ cover}{200} * day\ length)$$

(This assumes 100% cloud cover results in a 50% reduction in the level of irradiance).

7. Mean cloud: variable 6. averaged over the preceding three months.

Measures of the climatic variables were derived from the data presented in section 2.2.

4.3. Results

4.3.1. Disturbances

Major disturbances affected four of the 10 study sites during the two years of sampling. Site W1 experienced a sustained and unexplained drop in seagrass abundance from the start of sampling (July 1988) until sampling was abandoned at that site (July 1989). Total biomass decreased from 24.7 g/m² to 2.4 g/m² during that period. Site W2, located at the mouth of Tingalpa Creek, suffered from sedimentation on two occasions as a result of very high rainfall during April in 1989 and 1990 (Figure 2.4c). On each occasion the central 35 m of the transect was smothered with up to 5 cm of fine silt, which killed the seagrasses. Site E2 suffered from an unexplained die-off, which commenced around April 1989. Total biomass was reduced from 128 g/m² to 16 g/m² between January and July 1989. Site E4 was on the edge of an area intensively grazed by dugongs during August and September 1989 (Area 2, section 6.5.1.2) and part of the transect was heavily grazed. Due to the impacts of these disturbances on the seagrasses, post-disturbance data from these sites were not included in the analyses of seasonality.

Some sites were regularly grazed by dugongs (especially sites E7 and E8), but no individual grazing event was particularly intense, relative to the others. In fact, the Turtle Bank, where these sites occurred, was continually grazed, and this disturbance may maintain the seagrass community (see section 8.1). Data from these sites have been included in the analyses.

4.3.2. Seagrass abundance

4.3.2.1. Effect of year

Due to the loss of data resulting from disturbances, and the temporally unbalanced sampling regime, only three undisturbed sites were sampled on at least seven of the eight sampling occasions (Table 4.1). Sites E1, E5 and E8 were used to separate the effects of year and season. At these sites, there was no significant difference in the shoot density or total biomass of seagrass between year 1 (July 1988-April 1989) and year 2 (July 1989-April 1990). There was a significant seasonal effect, but no interaction between year and season (Table 4.2). On the basis of these results, seasonality was examined for all sites without regard for differences between years.

4.3.2.2. Effect of season

Seagrass biomass (both above- and below-ground) and shoot density varied significantly between seasons, sites and species, and these factors also interacted significantly (Table 4.3). Many of the significant interactions were due to the influence of a single species: the pattern of temporal change of Z. capricorni, which dominated many sites, contrasted with that of the other species. The results have been graphed to clarify the interactions (Figure 4.1).

Shoot density

A distinct, summer/autumn (January/April) peak in shoot density was displayed by three species of seagrass: H. spinulosa, H. ovalis and S. isoetifolium (Figure 4.1). In contrast, shoot density of Z. capricorni peaked in spring (October), when shoot density of the other four species tended to be lowest. The density of H. uninervis shoots did not peak until winter (July), although there was considerable overlap between seasons (Figure 4.1).

Above-ground biomass

Maximum above-ground biomass occurred during summer or autumn in all species (Figure 4.1).

Below-ground biomass

Every species showed an autumn peak in below-ground biomass (Figure 4.1). In contrast to the other species, Z. capricorni displayed a bimodal peak, with maxima in spring as well as autumn.

4.3.2.3. Amount of seasonal change

Table 4.4 summarises the seasonal change in abundance in each species. The greatest changes were shown by H. spinulosa, H. ovalis and S. isoetifolium. The least seasonal change in abundance was shown by Z. capricorni and H. uninervis. Averaging across species, shoot density increased by a factor of 1.9 (range 1.2 - 2.4), above-ground biomass by a factor of 2.3 (1.9 - 2.9) and below-ground biomass by 2.3 (1.5 - 3.1) between seasons with the minimum and maximum abundance.

4.3.2.4. Effect of site

Because of the atypical pattern of seasonal abundance displayed by Z. capricorni (above), the four sites dominated by Z. capricorni were graphed separately (Figure 4.2, at left) to the five sites dominated by other species (Figure 4.2, at right).

At sites without substantial proportions of Z. capricorni, shoot density peaked in summer (Figure 4.2a, at right), while total biomass lagged some months, peaking in autumn (Figure 4.2b, at right). At the sites dominated by Z. capricorni, the pooling of different species cancelled any seasonal pattern in seagrass abundance (Figure 4.2, al left).

4.3.3. Seagrass shoot length

The length of shoots varied significantly between seasons, sites and species, and these factors also interacted significantly (Table 4.5). To aid interpretation, the data have been graphed (Figure 4.3).

Although there was substantial variation between sites, there are some species-specific patterns. A summer/autumn peak in leaf length was shown by Z. capricorni, S. isoetifolium and H. uninervis (Figure 4.3). H. ovalis tended to have a weak autumn peak in shoot length. In contrast, the leaves of H. spinulosa reached their maximum length in winter, and were shortest in summer.

4.3.4. Above-ground biomass as a proportion of total biomass

In seagrasses at the inshore site W2, above-ground biomass was a larger component of total biomass than in seagrasses at sites in the East study area (Figure 4.4). This difference may be due to the increased turbidity of inshore waters (section 3.4.2.2). Additionally, the seagrasses at site W2 did not show the seasonal pattern displayed at the other sites (Figure 4.4).

Ignoring site W2, there were still significant interactions in the proportion of total biomass comprised of above-ground material (Table 4.6). Four species (H. spinulosa, H. ovalis, Z. capricorni and S. isoetifolium) displayed a summer peak in the proportion of total biomass contributed by the above-ground components (Figure 4.4). H. ovalis showed an additional peak in winter. H. uninervis displayed no seasonal pattern.

Pooling across seasons and sites, every species had significantly different proportions of above- and below-ground components (based on Least Significant Difference tests; Figure 4.5; Table 4.6). The Halophilae had the highest proportion of above- to below ground biomass (H. spinulosa: 0.56, SE = 0.006; H. ovalis: 0.48, SE = 0.005), while Z. capricorni (0.26, SE = 0.005) and H. uninervis (0.21, SE = 0.007) had the lowest. S. isoetifolium was intermediate (0.35, SE = 0.013; Figure 4.5).

4.3.5. The seasonal growth of each species

The previous results are synthesised below to provide a description of the presumed growth pattern of each species.

Halophila spinulosa

The flush of seasonal growth commenced in early summer. Shoot density and above- and below-ground biomass were lowest in spring but increased rapidly through summer to peak in autumn (Figure 4.1). Shoots were shortest in summer, when the new shoots were being generated. Shoots continued to lengthen until winter (Figure 4.3), but the density of shoots decreased faster than the shoots grew after autumn, so the biomass of leaves began to decline post autumn (Figure 4.1). To support the summer flush, the plants apparently shunted most of their resources into the leaves in summer, as this is the time when the leaves made up the greatest proportion of the total biomass (Figure 4.4), despite the short leaf length.

Halophila ovalis

The growing season commenced some time after spring. The density of shoots increased very rapidly to peak in summer (Figure 4.1). The biomass of shoots also peaked in summer (Figure 4.1), and although the density of leaves declined rapidly, the continued elongation of the leaves (Figure 4.3) maintained their high biomass through autumn. The increase in the biomass of the rhizomes lagged behind that of the leaves, peaking in autumn (Figure 4.1). This was reflected in the proportion of the total biomass that was made up of leaves: the proportion was high in summer (Figure 4.4), when there was a high density of new shoots, but it was low by autumn following the growth of rhizomes. Shoot density and biomass declined after autumn, and remained low through winter and spring (Figure 4.1).

Halodule uninervis

The relatively modest growth flush did not commence until summer, which was later than the response of the Halophilae. Both above- and below-ground components increased from January to peak in autumn, before declining rapidly to winter (Figure 4.1). The lengthening of shoots paralleled this seasonal pattern of growth (Figure 4.3). Due to the simultaneous increase in leaf and rhizome biomass, there was no seasonal change in their relative proportions (Figure 4.4).

Syringodium isoetifolium

The growing season commenced between spring and summer. Shoot density and shoot biomass increased rapidly through summer to peak in late autumn (Figure 4.1). The rhizomes were slower to respond, but increased very rapidly after summer, to peak in autumn (Figure 4.1). The above-ground:total biomass ratio reflected this staggered growth pattern: the above-ground components made up the largest proportion of total biomass in summer, before the rhizomes began to grow (Figure 4.4). The shoots increased in length rapidly after spring, but ceased growing after summer (Figure 4.3).

Zostera capricorni broad

Z. capricorni had a winter/spring growth period, which contrasted with the pattern of growth of the other four species. The growing period of Z. capricorni broad commenced in winter. Shoot density reached its peak in spring (Figure 4.1), when the new shoots were shortest (Figure 4.3). The leaves grew rapidly through to summer, when they reached their greatest length and greatest biomass. The density, length and biomass of the leaves then began to decline. The leaves were at their lowest density in autumn (Figure 4.1). The biomass of rhizomes was lowest in summer, when the biomass of shoots peaked, increased to autumn, as the above-ground components decreased and then declined to winter. The plants' resources were apparently shunted relatively rapidly between the above- and below-ground components. Consequently, biomass showed a bimodal peak, troughs being produced as resources were shunted into leaf elongation in summer,

and new shoot production in winter. This reciprocal, bimodal pattern was reflected in the ratio of above-ground:total biomass (Figure 4.4).

4.3.6. Dead rhizome

Dead rhizome material was measured during sampling periods 4, 5 and 6. At other times the dead material was separated from the live, but not weighed. Measurable amounts of dead rhizome were separated from Z. capricorni and Halophila species, while only trace amounts were recorded from H. uninervis and S. isoetifolium.

Zostera capricorni

Dead rhizome made up 49% (SE = 2.1) of the total biomass of rhizomes (live + dead roots and rhizomes). Both the absolute abundance of dead rhizomes and the ratio of the biomass of dead to live rhizome, showed a significant season by site interaction (Table 4.7). The amount and ratio of dead rhizomes of Z. capricorni was stable at two sites (E5 and E6), but varied greatly at two other sites (E3 and E4). At both of the latter sites, the amount and ratio of dead rhizomes responded in a reciprocal manner to the amount of live rhizome: during periods of high below-ground biomass, there was relatively little dead rhizome and vice-versa. These data suggest that below-ground biomass had a 3 month cycle between abundance peaks and troughs (Figure 4.1; although this is impossible to determine precisely with a 3 month sampling period). The reciprocal pattern described here, suggests an approximately three month cycle of rhizome decomposition.

Halophila species

The dead roots and rhizomes of H. spinulosa and H. ovalis could not be reliably separated, and were therefore pooled. Dead rhizome material constituted 17% (SE = 1.3) of the biomass of all rhizome material (live + dead roots and rhizomes).

The abundance of dead rhizomes and the ratio of dead to live rhizomes showed a significant season by site interaction (Table 4.7). Only site E8 showed a large

change in the content of dead rhizomes over time. In autumn, when the amount of live rhizome was high, the amount of dead rhizome was also high, but the ratio of dead rhizome was low. However, by spring, there was very little live or dead rhizome, but the ratio of dead to live rhizome was high.

4.3.7. Algae

As there was a significant year by season interaction in the abundance of epiphytic and macro-algae (Table 4.8), temporal change in the abundance of algae was examined over sampling periods (7), rather than seasons (4).

4.3.7.1. Epiphytic algae

There was a significant interaction between sampling period and site in the abundance of epiphytic algae (Table 4.9). Figure 4.6a indicates that the abundance of epiphytic algae varied greatly between sites, but there was also a strong seasonal pattern reflected across sites. Epiphytic algae were most abundant during spring and least abundant in autumn, the reverse of the growth pattern of the seagrasses.

The differences between sites were due largely to the different seagrasses present. Two species of seagrass, S. isoetifolium and H. spinulosa, support most of the non-encrusting epiphytic algae in Moreton Bay (pers. obs.). In the spring of 1988, large quantities of epiphytic algae were recorded from site E4 (Figure 4.6a), which is dominated by S. isoetifolium (Table 4.1). This peak was not repeated in 1989 because part of the site was heavily grazed by dugongs in mid 1989, and data from subsequent sampling periods were not included in the analyses. The abundance peaks at sites E5 and E6 in spring and summer 1989 were due to algae on H. spinulosa. Similar peaks did not occur in the previous year, perhaps because the water was warmer (see section 2.2).

4.3.7.2. Macro-algae

There was a significant interaction between sampling period and site in the

abundance of macro-algae (Table 4.9). Macro-algae occurred in more than trace amounts at one site only (E8). The main species was Caulerpa mexicana, although there were also small quantities of C. cupressoides. Caulerpa spp. showed a strong seasonal pattern of growth, with summer and autumn peaks in abundance (Figure 4.6b). While this pattern paralleled the growth pattern of the seagrass at site E8 (Figure 4.2), the relative abundance of the algae and the seagrass actually showed a reciprocal pattern between years. In year one, seagrass abundance was relatively high and algae abundance was relatively low. In year two there was only a small amount of seagrass, but a large amount of algae.

4.3.8. Climatic correlates of seagrass abundance

The three measures of seagrass abundance (shoot density and above- and below-ground biomass) were highly correlated with each of the climatic variables (Table 4.10), especially the measures of water temperature and day length. The climatic variables were highly inter-correlated, as several of them were measures of seasonality. So, although it is not possible to identify which climatic variable is most highly correlated with seagrass growth and abundance, it is apparent that the abundance of seagrass in the Moreton Bay study areas is closely related to the seasonal change in the climate.

Sites E7 and E8 showed the lowest correlations with the climatic variables (Table 4.10). These sites were located on the Turtle Bank, one of the areas most frequently disturbed by grazing dugongs (see section 8.1).

4.4. Discussion

4.4.1. Seagrass

Although seasonality was not detected in Moreton Bay seagrasses in some previous studies, probably due to small sample sizes (Boon, 1986; Young, 1978: some communities; Young and Kirkman, 1975: some communities), the results presented here show that the abundance of seagrasses in Moreton Bay followed a pronounced seasonal pattern. Seasonal changes in seagrass abundance would be

expected, due to the sub-tropical location of Moreton Bay. While seagrasses in tropical areas usually display a less prominant pattern of seasonality (Lanyon, 1991; Brouns, 1985a, 1987a and b; Brouns and Heijs, 1986; Mellors, 1991), a strong seasonal pattern is typical of temperate areas. In temperate Australian waters, a unimodal, summer peak in seagrass abundance has been described for H. ovalis (Hillman and McComb, 1988a cited in Hillman et al., 1989), Heterozostera tasmanica (Bulthuis and Woelkerling, 1983), Z. capricorni (Kirkman et al., 1982; Larkum et al., 1984) and Z. muelleri (Kerr and Strother, 1990). A similar pattern has been recorded for Halophila stipulacea (Wahbeh, 1988), Thalassia testudinum (Macauley et al., 1988), Z. marina (Jacobs, 1979; Orth and Moore, 1986; Roman and Able, 1988; Sand-Jensen, 1975) in northern temperate and subtropical waters. Some temperate species, however, show little seasonal change in abundance (Amphibolis antarctica at a subtropical site: Walker and McComb, 1988, Posidonia australis: Kirkman and Reid, 1979; West and Larkum, 1979).

4.4.1.1. Amount of seasonal change

The biomass of above-ground components varied seasonally by factors of 1.9 to 3.9, depending on the species of seagrass (Table 4.4). This compares with seasonal changes in above-ground biomass of about two-fold in tropical areas (Lanyon, 1991; Mellors, 1991). In temperate regions, a two to four fold difference is common, although much higher values have been recorded (H. ovalis: 2-4 fold, Hillman and McComb, 1988b cited in Hillman et al., 1989; Z. capricorni: 4 fold, Larkum et al., 1984; 2.5 fold, Kirkman et al., 1982; H. tasmanica: 2-4 fold, Bulthuis and Woelkerling, 1983; Z. muelleri: 7-40 fold, Kerr and Strother, 1990; Z. marina: 2.8 fold, Jacobs, 1979; 4 fold, Sand-Jensen, 1975).

The biomass of rhizomes and roots also varied seasonally, by factors of 1.5 to 3.1, depending on species (Table 4.4). Two of the five species monitored in Moreton Bay (H. ovalis and S. isoetifolium) showed greater seasonal change in the abundance of rhizomes than in the abundance of shoots, which is an unusual response. Lanyon (1991) concluded that there was little temporal change in the

rhizome and root biomass in a number of tropical species at Townsville. In Botany Bay, NSW, the biomass of rhizomes of Z. capricorni varied seasonally by a factor of 2.5, while shoot biomass varied by a factor of four (Larkum et al., 1984). At two sites in Swan Bay, Victoria, the changes in rhizome biomass of Z. muelleri were two- and four-fold, respectively, while the comparative figures for shoot biomass were seven-and 40-fold (Kerr and Strother, 1990). At other temperate Australian locations, no seasonal variation was found in the abundance of rhizomes of H. ovalis (Hillman and McComb, 1988a), Z. capricorni (Kirkman et al., 1982) or P. australis (Kirkman and Reid, 1979; West and Larkum, 1979). Only Jacobs (1979) has reported a greater seasonal change in rhizome biomass (5-fold, although roots showed only a 0.2-fold change) than leaf biomass (2-fold). Other studies on the same species, Z. marina, have generally reported only a two-fold change in rhizome biomass (Sand-Jensen, 1975).

On average, the total biomass of seagrass species in Moreton Bay varied by 230% between winter/spring and summer/autumn. For the seagrass-dependent dugongs, such variation in the availability of their staple diet may have significant ramifications (see section 6.6.3.1).

4.4.1.2. Ratio of above-ground to total biomass

The ratio of above-ground biomass to total biomass showed a seasonal pattern, with a summer peak in at least three species (Figure 4.4). Such a response appears to be independent of latitude, as a similar pattern has been described for H. uninervis and C. serrulata in tropical Australia (Lanyon, 1991) and for Z. muelleri in temperate Australia (Kerr and Strother, 1990). In most species, this summer peak reflects the lag between the summer growth phases of the above- and below-ground components (Figure 4.1). In Z. capricorni, however, this summer peak in the ratio of above-ground biomass leaf biomass:total biomass results from the unusual pattern of rhizome abundance (low in summer; Figure 4.1).

Growth pattern of Z. capricorni

Among the five species monitored, only Z. capricorni deviated from the general pattern of summer growth. The growth of Z. capricorni was not inhibited by cold water and/or short day length, and its growth phase commenced in winter. Hence, shoot density peaked in spring (the other species peaked in summer or autumn) and maximum shoot length and shoot biomass peaked in summer (the other species generally peaked in summer or autumn; Figures 4.1 & 4.3). In contrast with all other species, the biomass of rhizomes of Z. capricorni declined during summer (Figure 4.1).

There are two possible explanations for the different growth pattern shown by Z. capricorni. A high proportion of the total biomass of Z. capricorni is made up of rhizomes and roots (74%, SE = 0.5; Figure 4.5). The comparatively large reserve of resources (principally starch; King and Holland, 1986) stored in the rhizomes may allow Z. capricorni to shunt resources into leaf production as soon as the water temperatures/light levels begin to increase after winter. The rapid mobilisation of stored starch allows other plants (especially alpine species) to initiate rapid growth in the spring (Mooney and Billings, 1960; Bannister and Ward, 1981 both cited in King and Holland, 1986) and defoliation studies with the tropical seagrass T. testudinum indicate that leaf regeneration is supported by rhizome reserves (Dawes and Lawrence, 1979; Greenway, 1974). The stored starch reserves of this species also allow it to endure short-term environmental stresses (Zieman, 1975). Pirc (1985) found that Posidonia oceanica, which also has an unusual growth pattern (greatest production in early spring, falling away in early summer), was able to store considerable amounts of carbon and nitrogen in its rhizomes during summer and autumn, which it mobilised to support winter leaf growth. The seasonal change in the biomass of rhizomes of Z. capricorni supports this explanation: the biomass of rhizomes dropped in January, at the time when leaf length and leaf biomass reached their maximum values (Figures 4.1 and 4.3). In the other species of seagrasses in Moreton Bay, which have fewer rhizomatous reserves, resources required to support leaf growth may have to be steadily accumulated, thus accounting for the parallel changes in the biomass of leaves and rhizomes in these species (Figure 4.1).

A second explanation for the winter growth of Z. capricorni invokes differences in physiological tolerance to cold conditions. Most of the seagrasses that occur in Moreton Bay are essentially tropical in distribution. Four of the seven species are at the southern edge of their distribution in Moreton Bay (Figure 4.7). Two of the three species which extend beyond Moreton Bay reach their greatest abundance in the tropics. Only Z. capricorni is more abundant in sub-tropical and temperate waters than in tropical waters (see Coles et al., 1987 and West et al., 1989). It is probable, therefore, that the other species are stressed by the winter conditions in Moreton Bay, and cannot commence their growth phase until mid-spring. Z. capricorni, on the other hand, may be less stressed by the relatively mild Moreton Bay winter (compared with other areas within its range), and requires no lag between the end of winter and the start of its growth phase. Poiner (1984b) found that the growth of C. serrulata, a tropical species at the limit of its range in Moreton Bay, ceased during the winter months, while Z. capricorni showed little seasonal change in growth rate.

In light of its relative abundance in Moreton Bay (section 3.3.4), the winter growth of Z. capricorni means that the dugongs are provided with an extensive source of young shoots during spring, when the abundance of the other species is very low (see section 6.6.3). The high proportion of dead Z. capricorni rhizomes, however, may be a disincentive to foraging dugongs. Dead rhizomes of Z. marina, and probably Z. capricorni, are comprised primarily of structural carbohydrates (Kenworthy and Thayer, 1984), which are poorly digested by dugongs (Lanyon, 1991).

4.4.1.3. Dead rhizomes

The amount of dead rhizomes of Z. capricorni in Moreton Bay showed an inverse relationship with the amount of live rhizomes. The same relationship between the abundances of live and dead rhizome was reported for Z. marina in France (Jacobs, 1979). This inverse relationship, integrated with the three month cycle in the abundance of Z. capricorni rhizomes (Figure 4.1) suggests a cycle of similar duration for the decomposition of dead rhizomes. In North Carolina (latitude 36° N, compared with 28° S for Moreton Bay) 50% of the rhizomes of Z. marina

decomposed in the first three months, compared with only 50-60% in nearly six months (Kenworthy and Thayer, 1984).

The abundance of dead rhizomes of Halophila species paralleled the abundance of live rhizomes, suggesting a more rapid rate of decomposition. In the Caribbean (18° N) decomposition of the rhizomes of H. decipiens is very rapid, a loss of 50% of the original weight occurring within 3 days (Josselyn et al., 1986).

4.4.2. Algae

Epiphytic algae showed a cold weather growth phase with abundance peaks in spring. The epiphytic algae were more abundant in 1989 than in 1988 and the winter water temperatures during 1989 were significantly colder than during 1988 (section 2.2). The abundance of epiphytic algae on T. testudinum in Florida also peaked in winter and was negatively correlated with water temperature (Macauley et al., 1988). The abundance of invertebrate grazers, however, peaks in summer (Ogden, 1980), so grazing pressure may be responsible for the apparent winter peak in epiphytic algal abundance.

The macro-algae, C. mexicana and C. cupressoides showed a summer growth pattern, similar to that of the seagrasses. The algae at site E8 were also more abundant in the second year of monitoring, when there was less seagrass. This reciprocal pattern of abundance is probably due to the effects of selective feeding by the dugongs. Site E8 is regularly grazed, and dugongs actively avoid feeding on Caulerpoid algae in Moreton Bay (see section 6.6.2.1). Hence, gazing may allow the algae to expand, while the seagrasses are suppressed.

4.4.3. Correlation with climatic variables

Seagrass abundance was highly correlated with all the measures of climatic seasonality, particularly water temperature and day length (Table 4.10). Even rainfall, which probably only has a significant impact on the inshore, river-influenced sites, was strongly correlated with seagrass abundance. This is because rainfall was also strongly correlated with the other variables (r = 0.79-0.99).

The consistent strength and significance of the correlations (Table 4.10) emphasises the strong relationship between the seasonality of the climate and the seasonality of seagrass abundance in Moreton Bay. This is in contrast to tropical areas. Lanyon (1991) correlated five measures of climate with seagrass abundance at three sites near Townsville for only eight significant correlations out of 15. Similarly, Mellors (1991) correlated seagrass abundance at Green Island, north Queensland, with seven climatic variables for only three (out of seven) significant correlations. The less pronounced seasonality of tropical seagrasses has been attributed to the smaller seasonal changes in environmental factors in lower latitudes (Hillman et al., 1989). Lack of correlation between seagrass biomass and environmental variables is, however, not limited to tropical climates. Walker and McComb (1988) reported no significant correlations between light levels or water temperature and biomass of A. antarctica in Shark Bay, which is on a similar latitude to Moreton Bay.

Several environmental factors may affect the seasonal growth of seagrasses, including temperature, light, salinity, nutrients and currents (see Hillman et al., 1989 for a review of each). The most important factors seem to be water temperature and light, the relative importance of each varying with different studies (see Bulthuis, 1987: Table I). The role of each of these factors in governing the growth of seagrasses is difficult to determine as they are usually inter-correlated: the amount of incoming solar radiation largely determines the water temperature (see Figures 2.3a & 2.4b). From the dugong's perspective, the specific mechanism by which the seagrasses' growth is controlled is not important. The fact that the climate of Moreton Bay undergoes distinct seasonal changes, particularly in water temperature and day length, and that these changes correlate strongly with the abundance of seagrass (Table 4.10) is of most relevance.

4.4.4. Productivity

The value of a seagrass species as a food source for a grazer, such as a dugong, is only partly characterised by its seasonal biomass. The rate of primary productivity of the seagrass determines the extent to which it can support grazing,

and the extent to which the grazing will impact upon the seagrass.

As long as destructive over-grazing does not occur, grazing by dugongs will have a positive influence on community productivity by transfering energy from the seagrass leaves, upon which few species feed (Bell and Pollard, 1989), to detritus (from faeces and cropped leaves that escape ingestion; Thayer et al., 1982). The balance between total biomass, productivity and grazing pressure, however, is crucial. A Caribbean meadow of T. testudinum with an above ground biomass of 249 g/m² and a productivity of 6 g dw m⁻² d⁻¹ could support in excess of 42 urchins/m² (48 mm diameter) without over-grazing (Greenway, 1976). Yet a change in the balance of biomass, productivity and grazing can result in destruction of the seagrass meadow. At a temperate location (Botany Bay, Australia), some 45 ha of P. australis meadow with an above ground biomass of 228 g/m² and a productivity of 1.9 g dw m⁻² d⁻¹ (West and Larkum, 1979) were converted to bare sand and fibre mats by overgrazing by erupted populations of urchins (Larkum and West, 1990).

The standing crops (above- plus below-ground biomass multiplied by area) of seagrasses in the study areas have been described in Chapter 3, and the seasonal changes in biomass are reported above. Although there is only one published measure of seagrass productivity from Moreton Bay (Z. capricorni; Moriarty et al., 1985), the primary production of many seagrasses, including most of the species occurring in Moreton Bay, has been measured at other locations (Table 4.11).

Measures of seagrass primary production are usually expressed as g dry weight m⁻² d⁻¹ (or as g C m⁻² d⁻¹) and are partly biomass dependant. To compare different species, the ratio of production to biomass, or specific growth rate (SGR) is used. SGR is equivalent to turnover rate: the fraction of an organism or population that is produced per unit time. The reciprocal of SGR gives turnover time, which is the period required for crop replacement (Hillman et al., 1989; Zieman, 1975). Table 4.11 presents measures of the above-ground productivity of several seagrass species.

Surprisingly, there is little evidence that the rates of primary production differ between tropical and temperate locations (Table 4.11; Hillman et al., 1989). Some of the highest and some of the lowest SGRs occurred both in tropical and in temperate waters (Table 4.11). Given this lack of latitudinal pattern (although acknowledging the lack of comparative data on the same species from tropical and temperate regions), it is possible to cautiously extrapolate measures of productivity to Moreton Bay.

Data are available on the above-ground productivity of all but one (H. spinulosa) of the seven species of seagrass that occur in Moreton Bay. Given the consistency of the SGR values of three of its congenera (mid-points of 6.55, 6.65 and 6.8% per day; Table 4.11) I estimate the SGR of H. spinulosa to be 6% per day.

Table 4.12 presents an estimate of the net above-ground productivity of each species of seagrass in the two study areas of Moreton Bay. These estimates are based on the above-ground standing crop of each species of seagrass in the East and West study areas (Table 3.5) and the SGRs compiled in Table 4.11. The measure of Z. capricorni productivity in Moreton Bay made by Moriarty et al. (1985) could not be used as no biomass estimate was published, preventing the calculation of the SGR.

These estimates do not account for the seasonality of seagrass abundance, nor the seasonality of productivity. Productivity usually follows a seasonal pattern similar to, but more exaggerated than, biomass (Hillman et al., 1989). In temperate waters there is a summer peak in productivity (Bulthuis and Woelkerling, 1983; Hillman and McComb, 1988b; King and Holland, 1986; Kirkman et al., 1982; Kirkman and Reid, 1979; Larkum et al., 1984; West and Larkum, 1979). Seventy to ninety percent of annual growth occurs between spring (October) and autumn (April; Hillman et al., 1989). In tropical areas, productivity also peaks in summer, although the seasonality is less pronounced than in temperate areas (Brouns, 1987a). As with biomass, the differences in the seasonal patterns of productivity in tropical and temperate regions is attributed to greater changes in light and temperature at higher latitudes (Hillman et al., 1989).

One's perception of the seagrass system in the study areas, based on standing crop, is dramatically altered by the integration of the SGRs with the above-ground standing crops (Table 4.12). In terms of standing crop, both the East and West study areas were dominated by Z. capricorni (1,956 tonnes), and the contribution of the three species of Halophila was relatively minor (697 tonnes; Table 4.12 and Figure 3.3). Yet the estimated annual primary production of the Halophilae exceeds that of Z. capricorni: 15,866 t compared with 14,282 t (Table 4.12).

When the relative productivities of the rhizomes are taken into account, the importance of the Halophilae is further enhanced. The below-ground production of H. ovalis constitutes 50% of its total production (Hillman and McComb, 1988b cited in Hillman et al., 1989) while the rhizomes of Z. capricorni in Moreton Bay constitute only 15.6% of total production (excluding the roots; Moriarty et al., 1985). The above-ground productivity of other species that occur in Moreton Bay has been estimated to be 22-30%, 39% and 26% of the total production of H. uninervis, S. isoetifolium and C. serrulata respectively (Brouns, 1987a).

Although the species of Halophila occur at relatively low biomasses (Figure 4.1; Table 3.3), and account for only a modest proportion of the total standing crop of seagrass (Table 4.12; Figure 3.3), they play a crucial role in the community productivity of central Moreton Bay. Relatively little is known of the ecology of H. spinulosa and H. decipiens, but H. ovalis is a fast growing, colonising species that is able to tolerate physical disturbance and a wide range of environmental conditions (Birch and Birch, 1984; Brouns, 1987b; Hillman et al., 1989).

The importance of H. ovalis and the consequences of the seasonality of the biomass and productivity of seagrasses for the nutrition of dugongs of Moreton Bay will be discussed in Chapter 6.

Table 4.1. Characteristics of the 10 sites used to monitor temporal changes in the abundance of seagrasses in the Moreton Bay study areas and months of sampling at each site (*). 'D' indicates the approximate time of disturbance (see text).

Site	Study area	Seagrass community[1]	Seagrasses present (decreasing abundance)[2]	Depth (m)	Sampling period 1988 Jul 1	Oct 2	1989 Jan 3	Apr 4	Jul 5	Oct 6	1990 Jan 7	Apr 8
W1	West	H3	Hs Ho	-1.5	* D	*	*	*	*			
W2	West	H1	Hs Ho Zc	-0.1	*	*	*	D*	*	*	* D	*
E1	East	ZB3 & H1	Zc Hs Ho Hu	-0.4	*	*	*	*	*	*	*	*
E2	East	ZB3	Zc Ho	-0.2	*	*	*	D*	*	*		
E3	East	ZB1	Zc Hu Si	+0.6		*	*	*	*	*		
E4	East	ZB1	Si Hu	+0.8		*	*	*	* D	*	*	*
E5	East	H1	Hs Ho Zc	-0.4	*	*	*	*	*	*	*	*
E6	East	ZB5	Ho Hs Zc	-0.4	*	*	*	*	*	*		
E7	East	H5	Ho Hu	-0.5		*	*	*	*	*	*	
E8	East	H4	Ho Hu	+0.1		*	*	*	*	*	*	*

[1] Defined in Table 3.2.
[2] Hs: Halophila spinulosa; Ho: H. ovalis; Zc: Zostera capricorni; Hu: Halodule uninervis; Si: Syringodium isoetifolium

Table 4.2. Results of analyses of variance testing for the effect of year and season on the abundance of seagrass in Moreton Bay. Data from sites E1, E5 and E8 only were used.

Factor	Total Biomass df	MS	F	p	Shoot Density df	MS	F	p
Year[1]	1	110.0	0.13	0.7193	1	407423.4	2.41	0.1208
Season[1]	3	2522.4	2.96	0.0310	3	2643634.3	15.63	0.0001
Yr*Season	3	480.5	0.56	0.6385	3	201133.1	1.19	0.3124
Error	3492	851.5			1742	169130.1		
Total	3499				1749			

[1] Fixed factors

Table 4.3. Results of analyses of variance testing for the effect of season, site and species on the abundance of seagrass in Moreton Bay. The degrees of freedom reflect the unbalanced design.

Factor	df	Above-ground biomass			Below-ground biomass			Shoot density		
		MS	F	p	MS	F	p	MS	F	p
Season (Sn)[1]	3	12621	35.96	0.0001	47476	24.90	0.0001	8739541	14.96	0.0001
Site (St)[1]	8	5822	16.59	0.0001	104335	54.73	0.0001	26592450	45.51	0.0001
Species (Sp)[1]	4	22786	64.93	0.0001	99955	52.43	0.0001	36422182	62.33	0.0001
Season*Site	22	586	1.67	0.0259	5069	2.66	0.0001	1162108	1.99	0.0040
Season*Sp	12	1041	2.97	0.0004	5704	2.99	0.0004	2279003	3.90	0.0001
Site*Sp	13	30390	86.59	0.0001	222931	116.93	0.0001	49595220	84.88	0.0001
Sn*St*Sp	36	1274	3.63	0.0001	7847	4.12	0.0001	1414410	2.42	0.0001
Error	3551	351			1906			584301		
Total	3649									

[1] Fixed factors

Table 4.4. Factors by which mean seagrass abundance changed between seasons of minimum and maximum abundance at nine sites in Moreton Bay.

Species	Shoot Density	Biomass	
		Above-ground	Below-ground
H. spinulosa	2.4	2.9	2.6
H. ovalis	2.2	1.9	2.7
S. isoetifolium	2.0	2.2	3.1
H. uninervis	1.2	2.4	1.6
Z. capricorni	1.5	1.9	1.5

Table 4.5. Result of analysis of variance testing for differences in shoot length between seasons, sites and seagrass species in Moreton Bay. The degrees of freedom reflect the unbalanced design.

Factor	df	MS	F	p
Season[1]	3	59117	63.71	0.0001
Site[1]	7	4360	4.70	0.0001
Species[1]	4	92425	99.61	0.0001
Season*Site	19	8125	8.76	0.0001
Season*Species	12	10263	11.06	0.0001
Site*Species	6	5366	5.78	0.0001
Season*Site*Species	15	2059	2.22	0.0044
Error	3691	928		
Total	3757			

[1] Fixed factors

Table 4.6. Result of analysis of variance testing for the effect of season, site and species on the proportion of above-ground biomass to total biomass in seagrasses in Moreton Bay. Data from site W2 are not included. Data were arcsine transformed. The degrees of freedom reflect the unbalanced design.

Factor	df	MS	F	p
Season[1]	3	0.519	41.04	0.0001
Site[1]	7	0.088	7.01	0.0001
Species[1]	4	2.184	172.57	0.0001
Season*Site	20	0.036	2.87	0.0001
Season*Species	12	0.054	4.23	0.0001
Site*Species	8	0.055	4.34	0.0001
Season*Site*Species	23	0.023	1.79	0.0120
Error	1711	0.013		
Total	1788			

[1] Fixed factors

Table 4.7. Results of analyses of variance testing for the effect of season and site on the abundance of dead rhizome in seagrasses in Moreton Bay. The degrees of freedom reflect the unbalanced design.

Factor	Amount of dead rhizome				Ratio: dead to live rhizome			
	df	MS	F	p	df	MS	F	p
Zostera capricorni								
Season[1]	2	2191	1.22	0.2964	2	0.72	0.40	0.6704
Site[1]	3	135096	75.27	0.0001	3	8.9	4.90	0.0028
Season*Site	6	5586	3.11	0.0057	3	7.6	4.16	0.0007
Error	288	179			157	1.8		
Total	299				168			
Halophila sp.								
Season[1]	2	14.4	3.99	0.0193	2	49.2	18.44	0.0001
Site[1]	4	141.5	39.60	0.0001	4	102.4	38.36	0.0001
Season*Site	2	32.5	9.00	0.0001	8	41.1	15.41	0.0001
Error	360	3.6			309	2.7		
Total	374				323			

[1] Fixed factors

Table 4.8. Results of analyses of variance testing for the effect of year and season on the abundance of algae on Moreton Bay seagrass beds. The degrees of freedom reflect the unbalanced design.

Factor	Epiphytic algae				Macro-algae			
	df	MS	F	p	df	MS	F	p
Year[1]	1	1019.8	28.51	0.0001	1	31.2	2.10	0.1475
Season[1]	3	242.5	6.78	0.0002	3	64.7	4.36	0.0048
Yr*Season	2	20.33	5.68	0.0036	2	101.6	6.85	0.0012
Error	518	35.8			518	14.8		
Total	524				524			

[1] Fixed factors

Table 4.9. Results of analyses of variance testing for the effect of sampling period and site on the abundance of algae in Moreton Bay seagrass beds. The degrees of freedom reflect the unbalanced design.

Factor	Epiphytic algae				Macro-algae			
	df	MS	F	p	df	MS	F	p
Sampling period (SP)[1]	6	801.2	10.07	0.0001	6	59.6	10.02	0.0001
Site[1]	8	1165.1	14.64	0.0001	8	58.9	9.90	0.0001
SP*Site	30	933.6	11.73	0.0001	30	28.9	4.86	0.0001
Error	1080	79.6			1080	5.9		
Total	1124				1124			

[1] Fixed factors

Table 4.10. Parametric correlations (r) between three measures of seagrass abundance (shoot density and above- and below-ground biomass) and climatic variables. Due to differences in seagrass abundance between sites, each site was analysed separately. See text for an explanation of climatic variables. Mean values refer to preceeding three months. All correlations were highly significant ($p < 0.0001$).

Site	n	Climatic variables						
		Water temperature	Mean water temperature	Day length	Mean day length	Mean rain	Cloud	Mean cloud
Shoot density								
W2	75	0.8945	0.8845	0.8903	0.8860	0.8725	0.8921	0.8860
E1	200	0.9138	0.9195	0.9165	0.9197	0.7940	0.9122	0.9148
E2	75	0.9022	0.9040	0.9096	0.9099	0.9227	0.9110	0.9139
E3	125	0.9039	0.8996	0.9039	0.9032	0.7464	0.9023	0.9007
E4	100	0.9143	0.9222	0.9115	0.9176	0.7768	0.8989	0.9088
E5	198	0.8879	0.8962	0.8758	0.8847	0.6907	0.8578	0.8700
E6	149	0.8750	0.9004	0.8702	0.8846	0.7901	0.8489	0.8601
E7	131	0.6864	0.6939	0.6743	0.6801	0.4787	0.6710	0.6713
E8	169	0.7821	0.7964	0.7740	0.7828	0.6633	0.7628	0.7657
Above-ground biomass								
W2	75	0.8003	0.7912	0.7937	0.7900	0.7682	0.7939	0.7879
E1	200	0.8720	0.8803	0.8616	0.8698	0.7226	0.8487	0.8556
E2	75	0.9244	0.9395	0.9249	0.9324	0.9060	0.9157	0.9254
E3	125	0.8779	0.8816	0.8595	0.8666	0.6736	0.8516	0.8513
E4	100	0.8076	0.8169	0.7950	0.8048	0.6358	0.7782	0.7917
E5	198	0.8554	0.8663	0.8432	0.8540	0.6941	0.8212	0.8368
E6	149	0.8422	0.8719	0.8383	0.8552	0.8006	0.8130	0.8278
E7	131	0.7058	0.7265	0.6913	0.7048	0.5597	0.6752	0.6827
E8	169	0.7561	0.7853	0.7487	0.7646	0.7287	0.7266	0.7360
Below-ground biomass								
W2	75	0.6801	0.6723	0.6755	0.6723	0.6576	0.6763	0.6713
E1	200	0.7542	0.7622	0.7664	0.7672	0.7487	0.7630	0.7627
E2	75	0.9127	0.9200	0.9217	0.9245	0.9365	0.9210	0.9274
E3	125	0.9083	0.9064	0.8963	0.9002	0.7199	0.8890	0.8898
E4	100	0.8904	0.8996	0.8771	0.8875	0.7239	0.8580	0.8721
E5	198	0.8247	0.8391	0.8112	0.8245	0.6621	0.7854	0.8056
E6	149	0.7609	0.7842	0.7560	0.7708	0.6924	0.7323	0.7482
E7	131	0.6839	0.7086	0.6641	0.6808	0.5312	0.6443	0.6536
E8	169	0.7060	0.7328	0.6916	0.7086	0.6338	0.6681	0.6781

Table 4.11. Measures of above-ground productivity of selected seagrasses, ordered by latitude of study. Specific Growth Rate (SGR) is the ratio of production to biomass. See text for further definition of terms. All measures were derived by marking techniques. Data published as g C were converted to g dw by multiplying by 2.778. Data presented as ash-free dw were multiplyed by 1.389 (see Hillman et al., 1989 and Kirkman and Reid, 1979). A range of values indicates multiple sites.

Species	Occurs in Moreton Bay	Productivity (g m^{-2} yr^{-1})	Specific Growth Rate (% day^{-1})	Turnover time (days)	Latitude of study	Reference
Halodule uninervis (inter-tidal)	Yes	1411	4.1	24	9° S	Brouns, 1987a
Halodule uninervis (sub-tidal)	Yes	2383	5.4	19	9° S	Brouns, 1987a
Syringodium isoetifolium	Yes	2789	2.8	36	9° S	Brouns, 1987a
Cymodocea serrulata	Yes	1825	2.9-4.5	22-34	9° S	Brouns, 1987a
Cymodocea rotundata	-	1014	2.5-3.9	25-40	9° S	Brouns, 1987a
Thalassia hemprichii	-	667-1500	2.6-3.7	27.38	9° S	Brouns, 1985a
Enhalus acoroides	-	889	1.2-3.2	31-83	9° S	Brouns & Heijs, 1986
Thalassia testudinum	-	2192	2.4	42	18° N	Greenway, 1976
Halophila decipiens	Yes		3.3-10	10-30	18° N	Josselyn et al., 1986
Syringodium filiforme	-		5.8	17	18° N	Zieman et al., 1979
Halophila hawaiiana	-		6.8	15	21° N	Herbert, 1986
Thalassia testudinum	-	917	1-3	33-100	23° N	Zieman, 1975
Amphibolis antarctica	-	1194	1.1-2.7	37-91	26° S	Walker & McComb, 1988
Halodule wrightii	-	778	4.8-11	9-21	28° N	Virnstein, 1982
Halophila ovalis	Yes	694	4.1-9	11-24	32° S	Hillman & McComb, 1988b[1]
Zostera capricorni	Yes		0.9-1	96-112	33° S	King & Holland, 1986
Zostera capricorni	Yes	1528	2.1-3.1	32-47	34° S	Larkum et al., 1984
Posidonia australis	-	458-1139	0.8-1.1	91-125	34° S	West & Larkum, 1979
Heterozostera tasmanica	-	417-611	0.8-2.5	40-125	38° N	Bulthuis & Woelkerling, 1983
Zostera marina	-	528	1.3-2	50-75	41° N	Thorne-Miller & Harlin, 1984
Zostera marina	-	1111	1.2-1.8	56-83	49° N	Jacobs, 1979
Zostera marina	-	917	1.8	56	56° N	Sand-Jensen, 1975

[1] Cited in Hillman et al., 1989.

Table 4.12. Estimates of the net above-ground primary production of each species of seagrass in the East and West study areas of Moreton Bay. Annual production is based on the summer standing crops. Values of Specific Growth Rate (SRG) and standing crop come from Tables 4.11 and 3.5 respectively. The mid-point was used when a range of SGRs were available for a species. The SRG of <u>H. spinulosa</u> has been guessed (see text). Different morphs of the same species have been pooled.

Species	Above-ground standing crop (tonnes)	Specific Growth Rate (% day⁻¹)	Net primary production (t dw yr⁻¹)
East study area			
<u>Halophila ovalis</u>	224.85	6.55	5375.60[1]
<u>Halophila spinulosa</u>	293.45	6	6426.55
<u>Halophila decipiens</u>	2.62	6.65	63.59
<u>Zostera capricorni</u>	1514.28	2	11054.24
<u>Halodule uninervis</u>	529.79	4.75	9185.23
<u>Cymodocea serrulata</u>	33.43	3.7	451.47
<u>Syringodium isoetifolium</u>	180.23	2.8	1841.95
Total	2778.65		34398.65
West study area			
<u>Halophila ovalis</u>	72.00	6.55	1721.34
<u>Halophila spinulosa</u>	103.64	6	2269.72
<u>Halophila decipiens</u>	0.37	6.65	8.98
<u>Zostera capricorni</u>	442.19	2	3227.99
<u>Halodule uninervis</u>	5.85	4.75	101.42
Total	624.05		7329.45

[1] Above-ground standing crop (tonnes) * Specific Growth Rate * 365 days

Figure 4.1.

Seasonal variation (mean and SE) in the above- and below–ground biomass and shoot density of seagrasses in Moreton Bay.

- ■ Shoot density
- ○ Above ground biomass
- ▽ Below ground biomass

Axes:

Left: Biomass (g/m^2)
Right: Density $(shoots/m^2)$
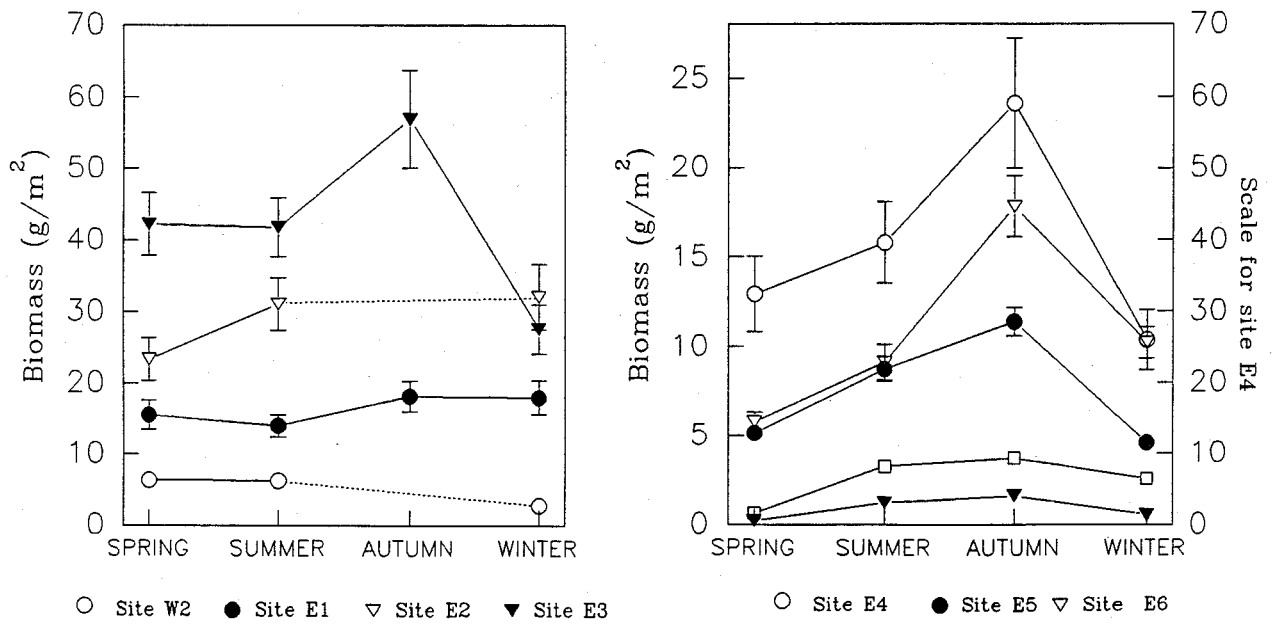
Spring was sampled in October, summer in January, autumn in April, winter in July.
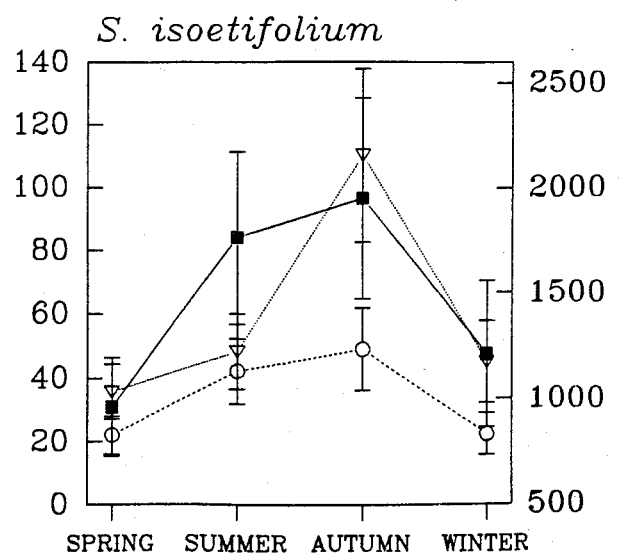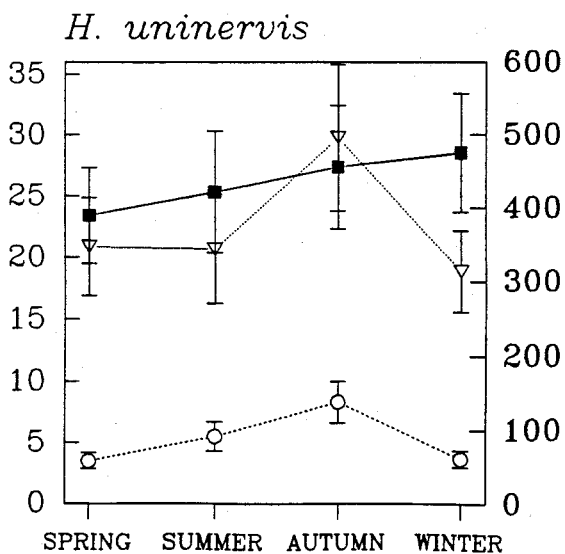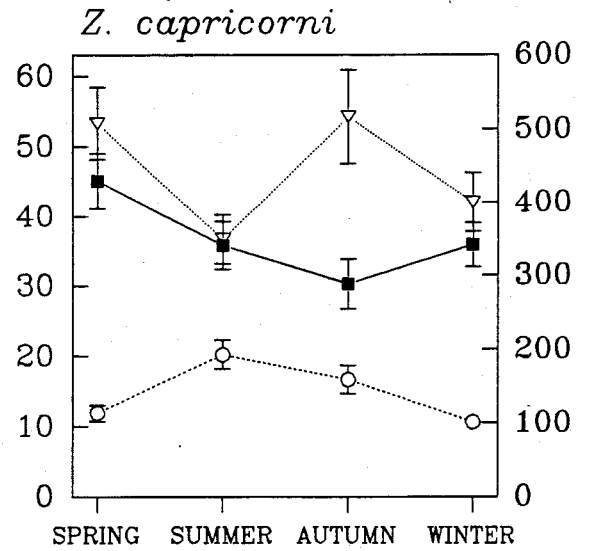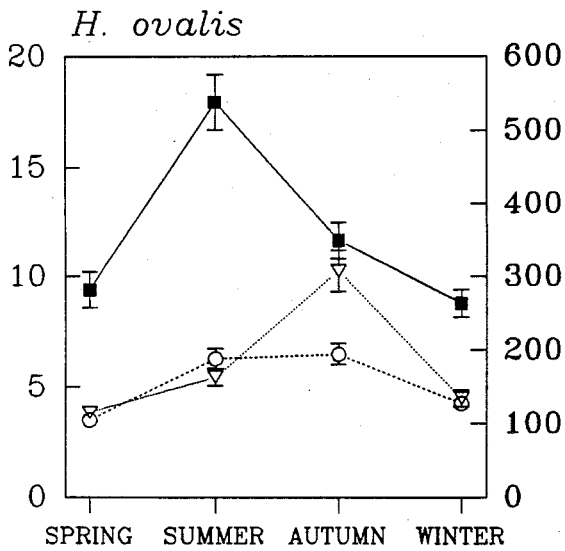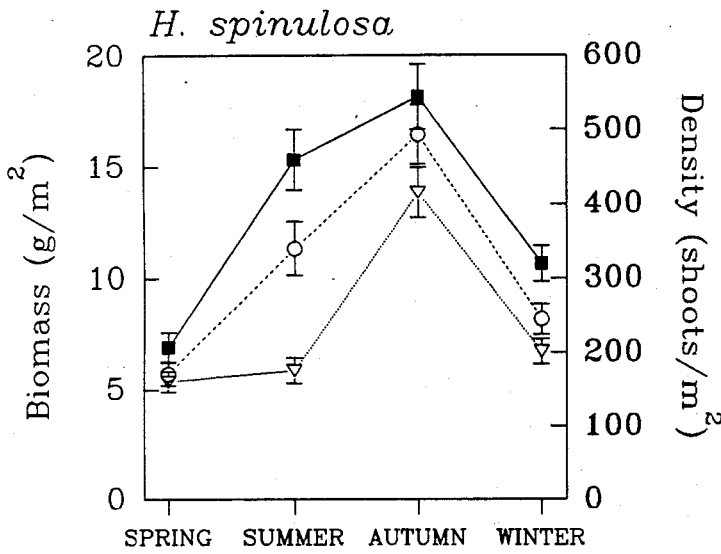
Figure 4.2. Seasonal variation (mean and SE) in (A) shoot density and (B) biomass (above- plus below-ground) of seagrasses at different sites in Moreton Bay.
Sites graphed on the left (W2, E1, E2 and E3) were dominated or co-dominated by *Zostera capricorni*.

A: Shoot density

O   Site W2   ● Site E1   ▽ Site E2   ▼ Site E3

O   Site E4   ● Site E5   ▽ Site E6
▼ Site E7   □ Site E8

B: Total biomass

O   Site W2   ● Site E1   ▽ Site E2   ▼ Site E3

O   Site E4   ● Site E5   ▽ Site E6
▼ Site E7   □ Site E8

H. spinulosa

Site E1 • ▽ Site E5 ▼ Site E6
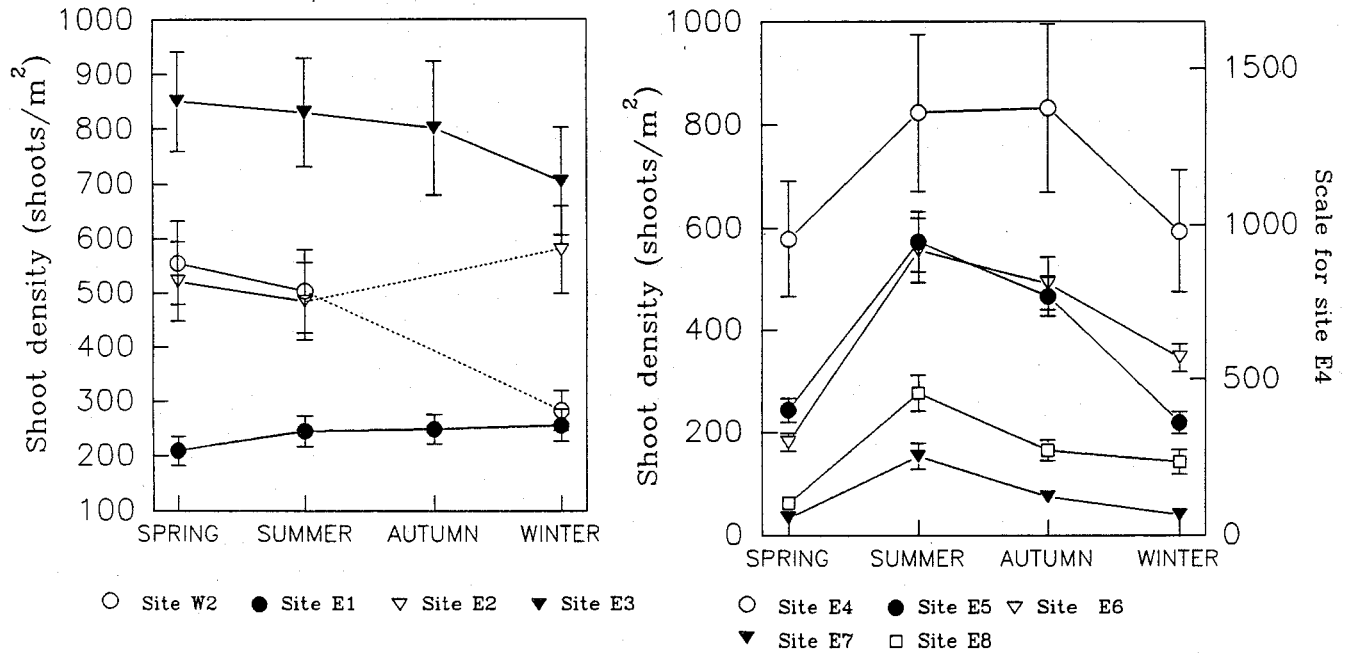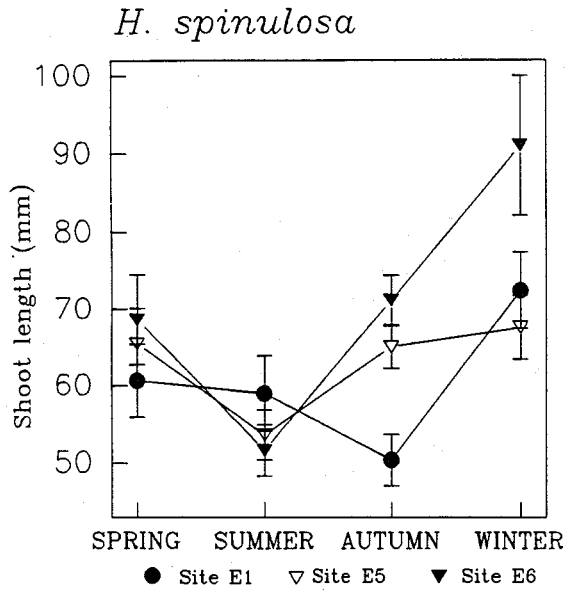
Figure 4.3. Seasonal variation (mean and SE) in the shoot lengths of seagrasses at different sites in the East study area in Moreton Bay.

H. ovalis

● Site E1   ▽ Site E5   ▼ Site E6   □ Site E7   ■ Site E8

Z. capricorni

● Site E1   ▽ Site E2   ▼ Site E3   □ Site E6

H. uninervis

○ Site E3   ● Site E4   ▽ Site E7   ▼ Site E8

S. isoetifolium

○ Site E3   ● Site E4

H. spinulosa

H. ovalis

Z. capricorni

H. uninervis

S. isoetifolium
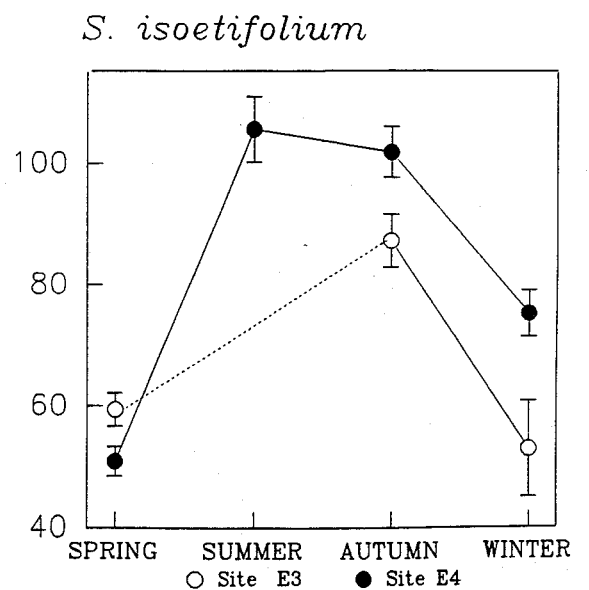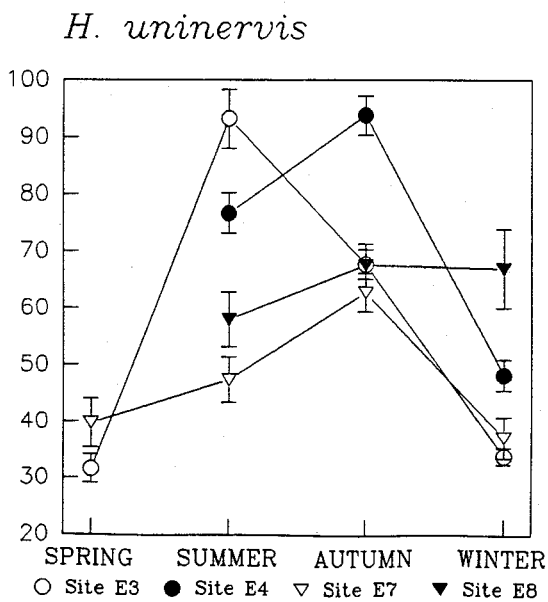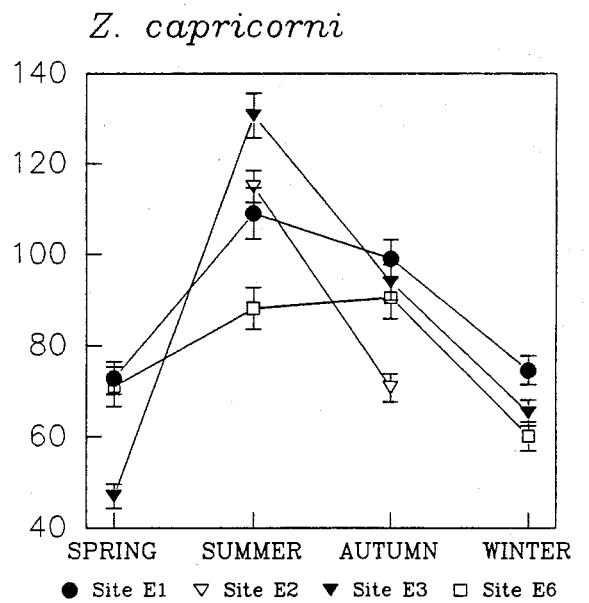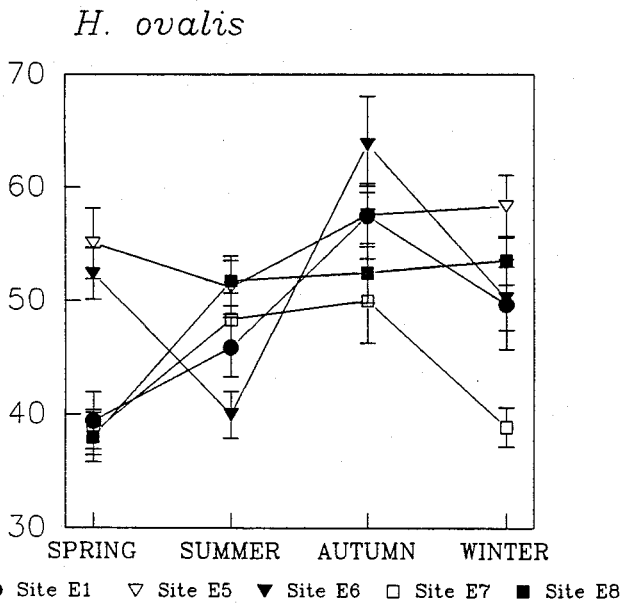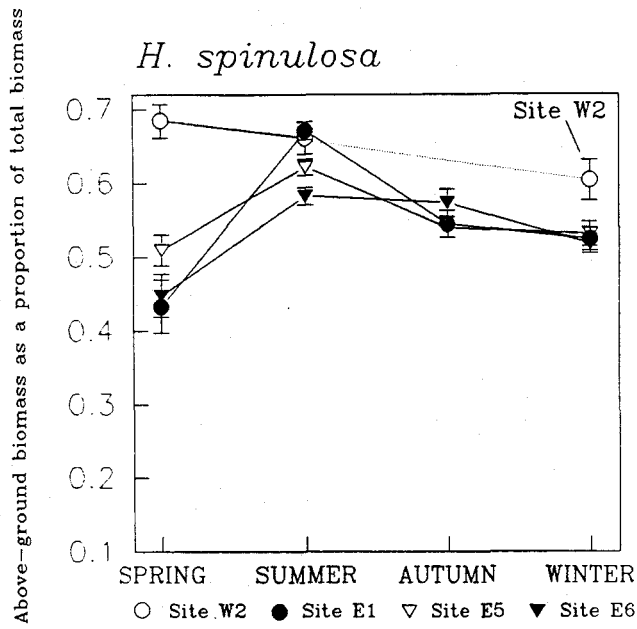
Figure 4.4. Seasonal variation (mean and SE) in above-ground biomass as a proportion of total biomass in seagrasses in Moreton Bay.
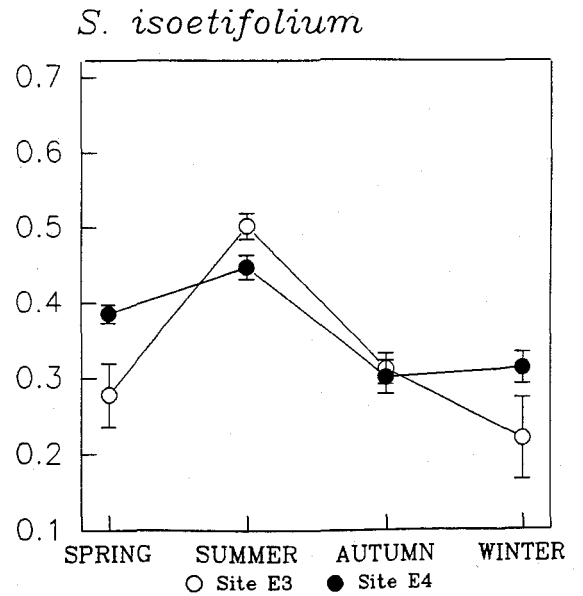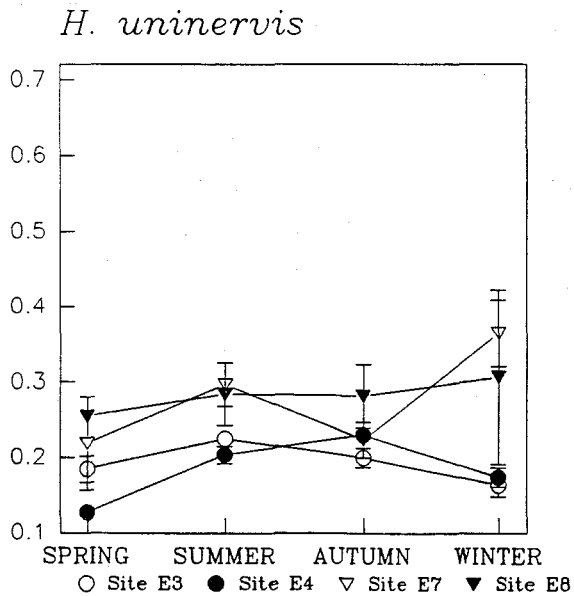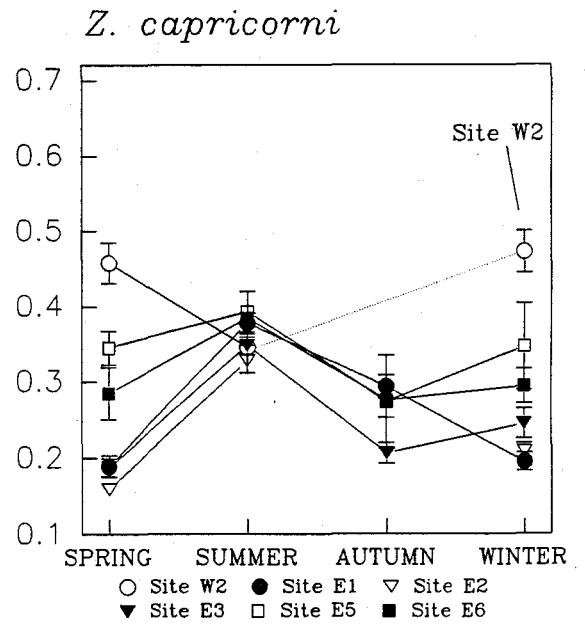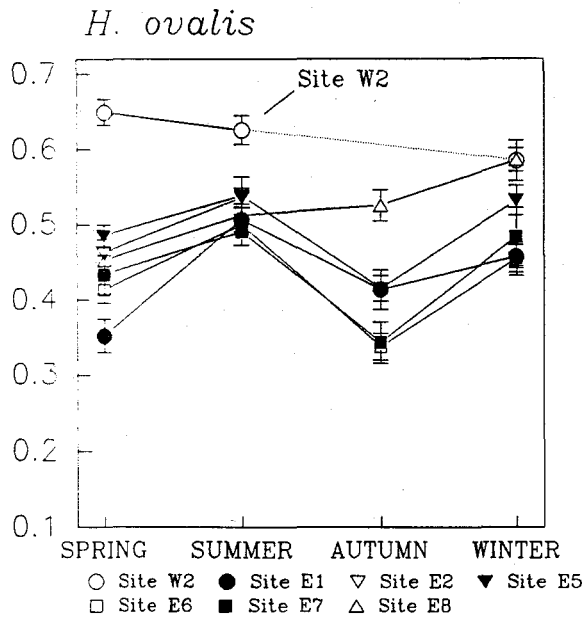
Figure 4.5. Relative contribution of the above– and below–ground components to the biomass of five species of seagrass in Moreton Bay.

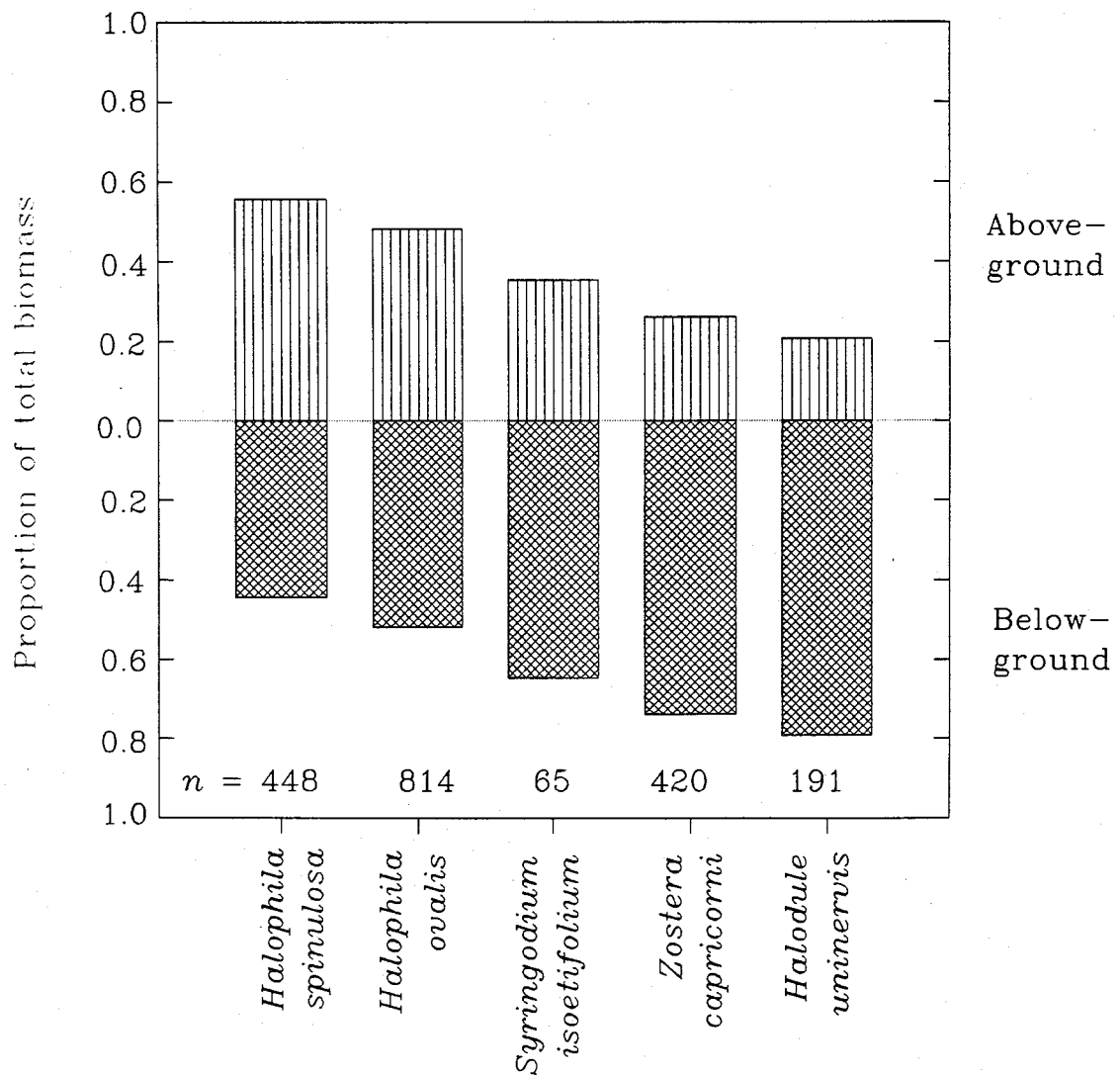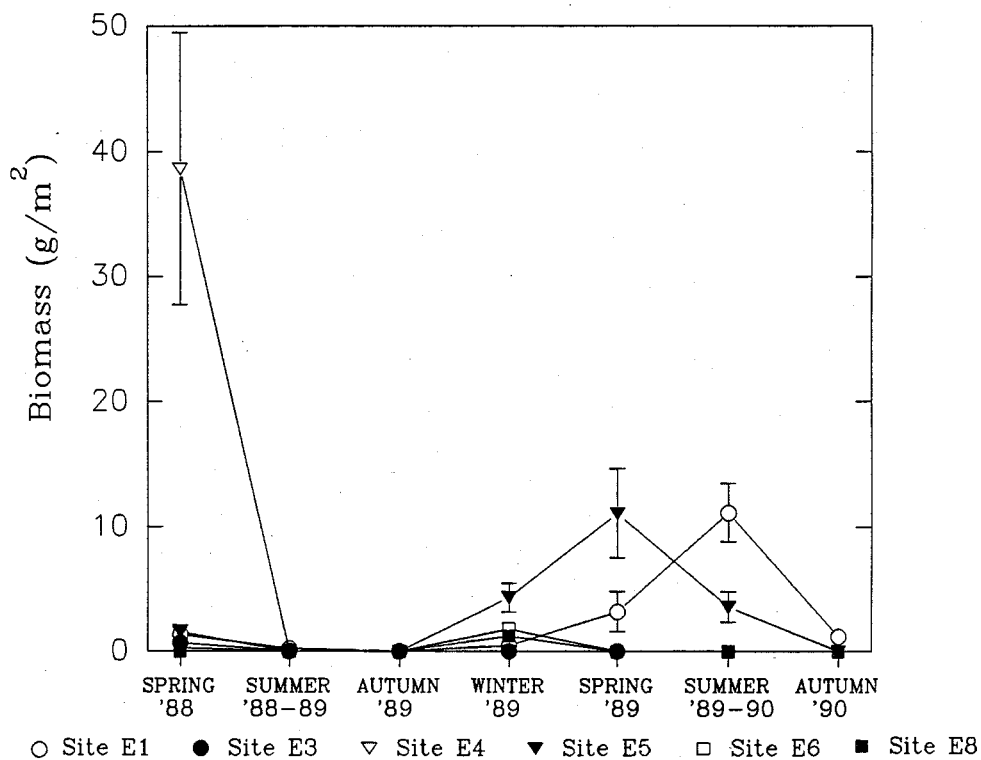Figure 4.6. Temporal change in the biomass (mean and SE) of (A) epiphytic and (B) macro-algae at different sites in the East study area of Moreton Bay.

A   Epiphytic Algae

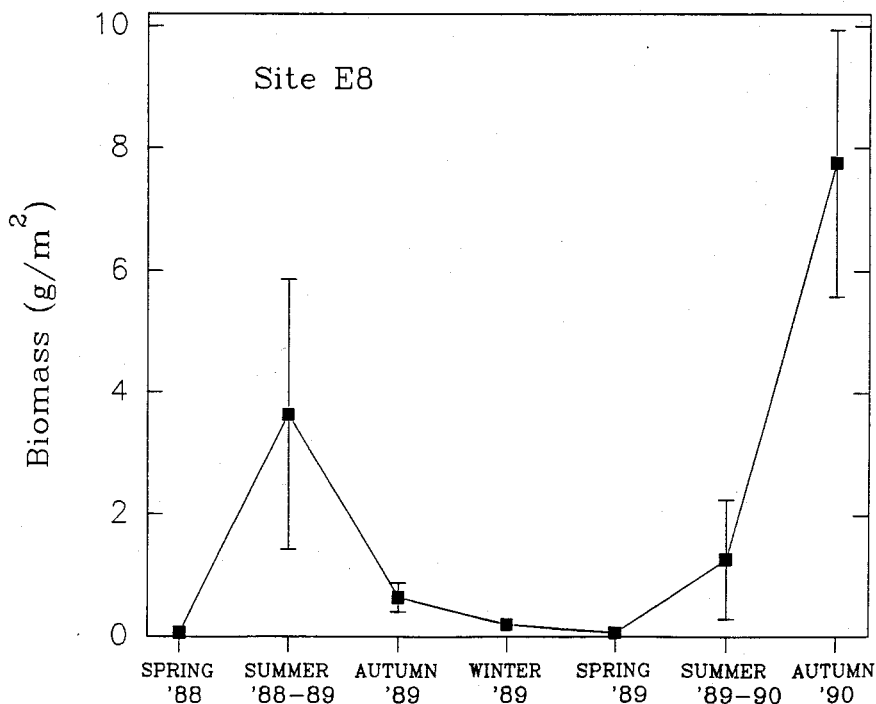| O Site E1 | ● Site E3 | ▽ Site E4 | ▼ Site E5 | □ Site E6 | ■ Site E8 |

B   Macro-algae

Figure 4.7. Limits of the eastern Australia distributions of
seagrasses that occur in Moreton Bay.
Sources: Bridges et al. (1982), Walker and Prince (1987)
and West et al. (1989).