

Seagrass distribution, community structure and productivity for Orman Reefs, Torres Strait – March and November 2004



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EXECUTIVE SUMMARY

The Torres Strait has some of the most extensive seagrass meadows in northern Australia. These meadows support populations of threatened species such as dugong and turtle as well as commercially and traditionally important fisheries. The Orman Reefs area of the central Torres Strait has been identified as one of the most important areas of seagrass habitat in Torres Strait and Queensland for dugong populations. This study describes in detail the seagrass distribution, abundance and community structure at Orman Reefs in March and November 2004 and uses this information to provide an estimate of the above ground-productivity and carbon assimilated by the seagrass meadows at the likely seasonal extremes of seagrass abundance.

An extensive coverage of seagrass was found within the Orman Reefs survey area in both March and November 2004. Seagrass covered the majority of the intertidal reef top areas and a large proportion of the subtidal areas examined. There were marked differences in seagrass above ground biomass (density), distribution and species composition between the two surveys with seagrass covering 18,700ha in March and 21,600ha in November. Seagrass biomass declined substantially in intertidal meadows between March and November but increased or remained unchanged for subtidal meadows. Changes to seagrass meadows were most likely a result of greater tidal exposure of intertidal meadows prior to November leading to desiccation and temperature related stress.

Above ground productivity and carbon assimilated by Orman Reefs seagrass meadows were a function of seagrass species composition, shoot density and size of meadows. Seasonal changes had a strong influence on all three of these factors and consequently had a strong effect on the total above ground production (259.8 t DW day⁻¹ in March and 111.5 t DW day⁻¹ in November) and carbon incorporated (89.4 tonnes day⁻¹ March and 38.0 tonnes day⁻¹ November) by Orman Reefs meadows. The majority of this production came from the intertidal meadows which accounted for 81% of the total production in March and 63% in November. The net above ground productivity of Orman Reefs meadows was high compared with other tropical seagrass areas that have been studied and was also higher than many other marine, estuarine and terrestrial plant communities.

The seagrass meadows of Orman Reefs are likely to be a significant resource to the region as they are one of the largest areas of shallow seagrasses described in northern Australia. These highly productive meadows are likely to be of key importance to fisheries, dugong and turtle in the central Torres Strait as well as a key source of carbon for associated ecosystems.

The results of this report form the basis of a paper that has been submitted for publication in a Torres Strait special edition of the Journal of Continental Shelf Research. That article should be consulted for a detailed discussion of the scientific issues raised in this report.

INTRODUCTION

Background

Seagrass meadows are of great ecological importance and have been recognised as one of the most productive marine ecosystems (Mann, 1973; McRoy and McMillan, 1977; Brouns and Heijs, 1985; Duarte and Chiscano, 1999). Globally, seagrass meadows are classified as one of the most valuable habitats for ecosystem services on a per hectare basis, preceded only by estuaries and swamp/flood plains (Constanza *et al.* 1997). Seagrass meadows are often the dominant primary producers in coastal areas, playing a key role in trophodynamics, habitat provision, substrate stability and biogeochemical cycling (McRoy and Helfferich 1977; Staples *et al.* 1985; Brouns and Heijs, 1985; Blaber *et al.* 1989; Haywood *et al.* 1995). Coastal areas containing seagrass meadows have also been closely linked with high fisheries production, principally due to their value as a nursery habitat (e.g. Coles *et al.* 1993; Watson *et al.* 1993). In tropical areas, direct herbivory of seagrasses by dugong and sea turtles is common (Lanyon *et al.* 1989) and many tropical seagrass species have high primary production rates (Mateo *et al.* 2006). There is also an assumption that seagrasses provide a substantial proportion of the primary productivity for associated ecosystems (Mateo *et al.* 2006; Kaldy *et al.* 1999).

Seagrass meadows can be highly dynamic, changing as a result of both natural and anthropogenic influences. In South East Asia, the biomass and growth of seagrasses can vary by up to a factor of four during one year (Brouns 1985; Erfemeijer and Herman 1994; Lanyon and Marsh 1995). There are a variety of factors that influence seagrass meadow biomass, area, and species composition including: physical disturbance (Duarte *et al.* 1997), herbivory (Klumpp *et al.* 1993), intraspecific competition (Rose and Dawes 1999), nutrients (Short 1988) and flooding (Campbell and McKenzie 2004). The most common changes, however, occur as a result of seasonal factors. Seasonal changes in light and temperature are key drivers controlling seagrass biomass (Duarte *et al.* 2006), species composition (Bridges *et al.* 1982) and productivity (McRoy and McMillan 1977) as they are critical in controlling photosynthesis (McRoy and Mc Millan 1977). Investigations of intra-annual variation in a tropical reef top seagrass habitat in north Queensland found both day length and maximum air temperature were positively correlated with the monthly seagrass standing crop (Mellors *et al.* 1993). While increases in light and temperature can be beneficial to seagrass growth, both of these factors, at their extremes, can also contribute to seagrass decline (Campbell *et al.* 2006; Roelofs *et al.* 2006). The influence of seasonal factors on seagrasses also varies between species. Marbà *et al.* (1996) reported that the growth of large species were less affected by environmental factors than smaller species. Similar trends have been found for seagrasses in tropical Queensland with intra-annual variability tending to be higher in meadows dominated by small growing *Halophila* and *Halodule* species (McKenzie *et al.* 1998; Rasheed *et al.* 2006).

The Torres Strait has some of the most extensive seagrass meadows in northern Australia. These meadows support populations of threatened species such as dugong and turtle as well as commercially and traditionally important fisheries (Lee Long *et al.* 1993). The people of the Torres Strait are highly reliant on fisheries as a source of food and income and the traditional fishing of dugong and turtle is also culturally important. The central Torres Strait region is particularly important and has been referred to as a “powerhouse” for dugong in the Torres Strait due to the extensive seagrass meadows in the area and the high number of dugong they support (Marsh *et al.* 2004). It is assumed that the primary production from the extensive seagrass meadows in the Torres Strait underpins much of this fisheries production. While it is generally accepted that seagrasses have an important role in primary

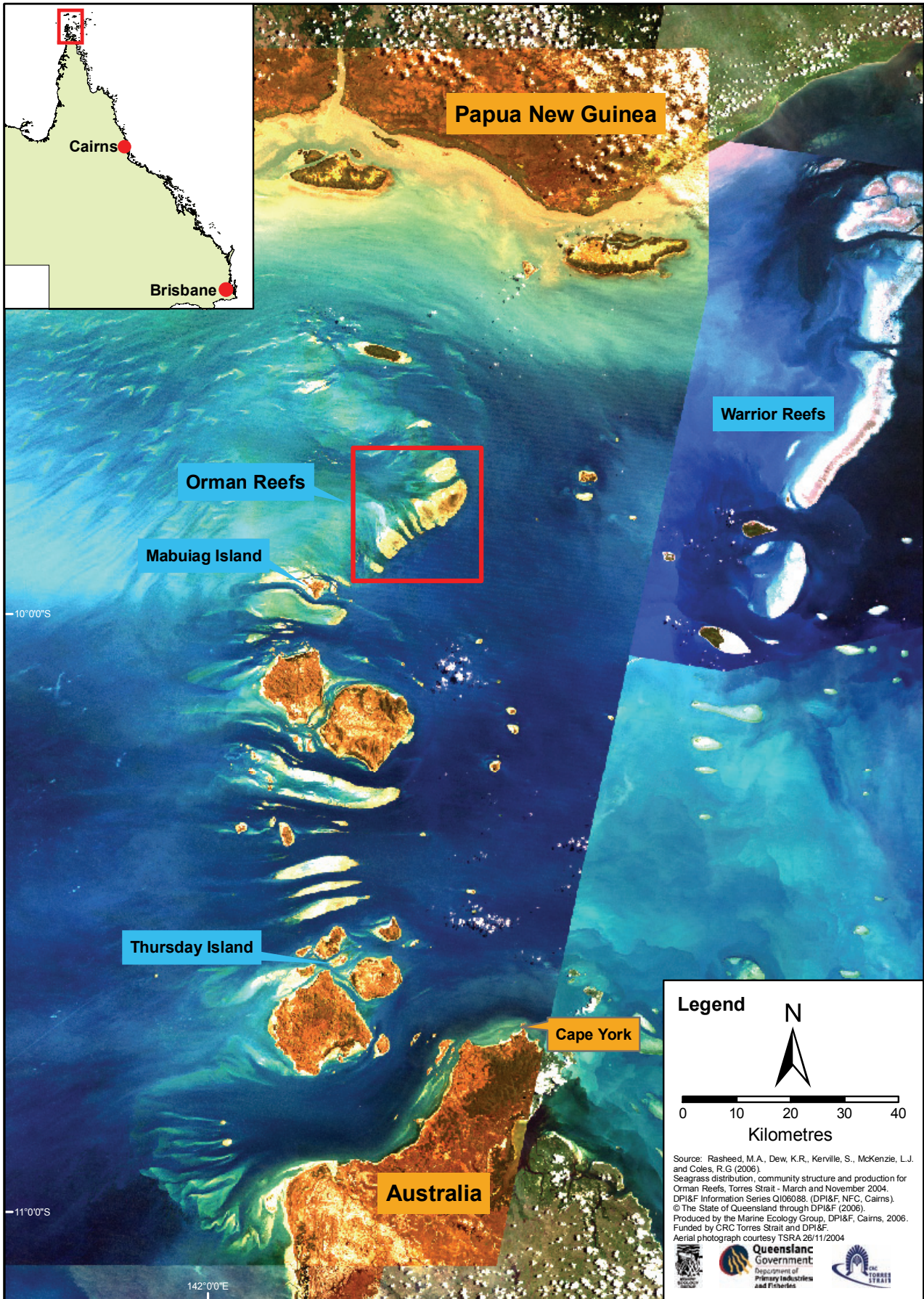
production in coastal marine ecosystems, and the production and growth rates of many individual species have been measured (eg. Kenworthy *et al.* 1989; Bandeira 2002; Erftemeijer *et al.* 1993; Uku and Björk 2005) there have been few studies that have attempted to measure the production of entire meadows or regions. No previous studies have attempted to determine the primary production of Torres Strait seagrass meadows.

The dynamics of seagrasses in the Torres Strait are strongly influenced by extremes in weather such as flood and cyclones. Studies have shown substantial seagrass dieback (up to 60%) in central Torres Strait associated with flooding (Long and Skewes 1996). These diebacks have been linked to declines in the population of dugong (Marsh *et al.* 2004). Lack of detailed, fine-scale studies which map and quantify seagrass abundance in the central Torres Strait has limited our ability to predict the consequences of disturbances on seagrass habitats and their associated ecosystems and fisheries.

The focus of the present study was to map and quantify seagrass communities in the Orman Reefs system of the central Torres Strait and assess the above ground production of these seagrass meadows during the two seasonal extremes. The specific objectives were to:

1. Describe and map seagrass species distribution and abundance at Orman Reefs in the wet and dry seasons;
2. Assess the above ground production and estimate the carbon produced by the seagrass meadows of Orman Reefs.

Map 1: Orman Reefs survey locality



Site Description

Torres Strait is situated between Papua New Guinea and Australia's most northern point. There are over 100 islands located in the Torres Strait, 18 of which are inhabited. The region is tropical and experiences a summer wet season and winter dry season. The majority of the annual rainfall (average 1,717 mm) falls during the wet season between December and April. Mean daily temperatures range from a minimum of 22.7°C in July to a maximum of 32.1°C in October. Water temperatures around Thursday Island to the south of Orman Reefs range between 24.4 and 27.7°C (Pitcher *et al.* 2004), however water temperatures are likely to be higher in the central Torres Strait region. Prevailing winds vary seasonally with southeast winds predominant during the dry season and northwest monsoons during the wet (Long and Poiner 1997).

The Orman Reefs are located in the central region of the Torres Strait, approximately 10 kilometres northeast of Mabuiag Island (Map 1). The central region of the Torres Strait is characterised by shallow waters (<20 metres) with small rocky islands fringed by reef. Coral cays with mangroves are found on some of the larger reefs (Long and Poiner 1997). The Orman Reefs system is comprised of six individual reefs with the four main reefs of Beka, Kai, Gariar and Anui comprising the majority of the reef area. While the reefs have a coral fringe the dominant habitat type on the majority of the reef top areas is seagrass.

METHODOLOGY

Seagrass surveys of Orman Reefs were conducted in March and November, 2004. The survey had two major components: an intertidal and shallow subtidal survey of seagrass distribution and community structure, and above ground productivity (growth rate) assessment of seagrasses.

1. SEAGRASS DISTRIBUTION AND COMMUNITY STRUCTURE

Orman Reefs seagrasses were mapped and assessed in both March (wet season) and November (dry season) 2004 to provide an indication of intra-annual variation in distribution and abundance. A variety of sampling methods were used based on the physical characteristics of the area being surveyed such as water depth, size of area to be surveyed and safety constraints. Three sampling techniques were used:

Intertidal seagrass

The large intertidal reef top areas were surveyed by helicopter at low tide when meadows were exposed. Boundaries of intertidal meadows were mapped during a low level flight of the meadows using GPS (Plate 1). The position of submerged areas likely to contain seagrass were also noted to help focus effort during the boat-based subtidal surveys. Sites to determine seagrass habitat characteristics were randomly chosen throughout the intertidal areas that were mapped using the helicopter. Sampling sites were examined from the helicopter hovering within a metre above the seagrass meadow. Sampling intensity was stratified with a greater number of sites located in areas where habitat complexity was high.

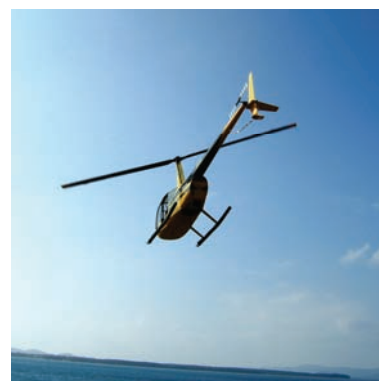


Plate 1 Helicopter intertidal mapping of exposed seagrass at spring low tide

Shallow subtidal seagrass

In subtidal areas, seagrass habitat characteristics were determined at sites located approximately every 500m on transects that extended from the intertidal edge of the reefs to the limit of the survey (approximately 1 nautical mile from the reef edge). Transects were spaced from 1 to 3 km apart with a higher density of transects in areas of high habitat complexity. Additional sites were sampled between transects to check for seagrass habitat continuity. Sites were examined by free-diving observers swimming to the bottom.



Plate 2 Subtidal seagrass at Orman Reefs

Deep subtidal seagrass

In subtidal areas where water was too deep for effective sampling by free-divers (>7m) an underwater CCTV camera system was used to assess seagrass habitat characteristics. The camera was deployed to the seabed and provided real-time footage to an observer on the boat. A Van Veen grab (grab area 0.0625 m²) was used at each site to confirm seagrass species and sediment characteristics. Seagrass habitat characterisation sites were located on transects and between transects in the same manner as the shallow subtidal diver sites.

Seagrass Habitat Characterisation Sites

Seagrass habitat characterisation sites encompassed a circular area of the substratum of approximately 10m². The position of each site was recorded using a Global Positioning System (GPS) accurate to ± 5 m. While methods of observing habitat characterisation sites varied (helicopter/diver/camera), information collected at each site was consistent. This included seagrass species composition, seagrass above ground biomass, depth below mean sea level (MSL) (for subtidal sites) and sediment type.

Seagrass above ground biomass was determined using a modified “visual estimates of biomass” technique described by Mellors (1991). This technique involves an observer ranking seagrass biomass in the field in three random placements of a 0.5m² quadrat at each site. Ranks were made in reference to a series of quadrat photographs of similar seagrass habitats for which the above ground biomass has previously been measured. This method was utilised for both the subtidal and intertidal survey areas. Three separate biomass ranges were used, low-biomass, high-biomass and a separate range for sites dominated by the two largest species, *Enhalus acoroides* and *Thalassodendron ciliatum*. The relative proportion of the above ground biomass (percentage) of each seagrass species within each survey quadrat was also recorded. Field biomass ranks were then converted into above ground biomass estimates in grams dry weight per square metre (g DW m⁻²). At the completion of sampling each observer ranked a series of calibration quadrats that represented the range of seagrass biomass in the survey for each of the three biomass ranges. After ranking, seagrass in these quadrats was harvested and the actual biomass determined in the laboratory. A separate regression of ranks and biomass from these calibration quadrats was generated for each observer and applied to the field survey data to determine above ground biomass estimates.

Seagrass Habitat Mapping

All data were entered into a Geographic Information System (GIS). Rectified colour aerial photographs of the Torres Strait (courtesy of TSRA), combined with aerial photography and videotape footage taken from the helicopter during surveys assisted with mapping. Other information including depth below MSL, substrate type, the shape of existing geographical features such as reefs and channels, was also interpreted and used in determining habitat boundaries.

Two GIS layers were created in ArcGIS[®] to describe Orman Reefs seagrasses:

- **Survey sites** - dGPS sites containing all data collected at seagrass survey sites;
- **Seagrass community types and density** - area data for seagrass meadows and information on community characteristics. Community types were determined according to overall species composition. A standard nomenclature system was used to name each of the meadows in the survey area. This system was based on the percent composition of biomass contributed by each species within the meadow (Table 1). Density categories for each meadow were determined by the mean above ground biomass of the dominant species (Table 2).

The precision of determining seagrass meadow boundaries was dependent on the range of mapping information and methods available for each meadow. Intertidal meadow boundaries had the highest precision. Large subtidal areas where meadow boundaries could not be seen from the surface had the lowest mapping precision. Boundaries of these meadows were based on the mid-point between the last site where seagrass was present and the next non-seagrass site.

Each meadow was assigned a mapping precision estimate (in metres) based on mapping methodology utilised for that meadow (Table 3). Mapping precision for seagrass meadows ranged from $\pm 50\text{m}$ for small isolated seagrass meadows to $\pm 200\text{m}$ for some subtidal meadows (Table 3). The mapping precision estimate was used to calculate a range of meadow area for each meadow and was expressed as a meadow reliability estimate (R) in hectares. Additional sources of mapping error associated with digitising and rectifying aerial photographs and with GPS fixes for survey sites were assumed to be embedded within the meadow reliability estimates.

The presence or absence of seagrass at each site was defined by the above ground biomass. Where above ground biomass was absent, the presence of rhizome/root and seed bank material was not reported. Survey sites with no seagrass can be found within meadows because seagrass cover within meadows is not always uniform and may be patchy and contain bare gaps or scars.

Table 1 Nomenclature for community types in Orman Reefs, March and November 2004.

Community type	Species composition
Species A	Species A is 90-100% of composition
Species A with Species B	Species A is 60-90% of composition
Species A with Species B/Species C	Species A is 50% of composition
Species A/Species B	Species A is 40% - 60% of composition

Table 2 Density categories and mean above ground biomass ranges for each species used in determining seagrass community density in Orman Reefs, March and November 2004.

		Density Category		
		Light	Moderate	Dense
Mean above ground biomass (g DW m ⁻²)	<i>H. uninervis</i>	<1	1.1 - 3.9	>4
	<i>H. ovalis</i>	<1	1.1 - 4.9	>5
	<i>H. decipiens</i>	<1	1.1 - 4.9	>5
	<i>H. spinulosa</i>	<15	15 - 35	>35
	<i>C. serrulata</i>	<5	5.1 - 24.9	>25
	<i>S. isoetifolium</i>	<5	5.1 - 24.9	>25
	<i>E. acoroides</i>	<40	40.1 - 99.9	>100
	<i>T. hemprichii</i>	<15	15.1 - 34.9	>35
	<i>T. ciliatum</i>	<40	40.1 - 99.9	>100
	<i>C. rotundata</i>	<5	5.1 - 24.9	>25

Table 3 Mapping precision and methodology for seagrass meadows in Orman Reefs, March and November 2004.

Mapping precision	Mapping methodology
50m	Small isolated subtidal meadow with boundaries determined by diver surveys; Inshore boundaries interpreted from survey sites and aerial photography.
100m	Meadow boundaries interpreted from helicopter surveys; All meadows intertidal; Recent aerial photography and satellite imagery aided in mapping.
200m	Meadow boundary determined by subtidal diver and video sites; Subtidal meadows only; Some depth information available for boundary determination.

2. ABOVE GROUND PRODUCTIVITY OF ORMAN REEFS SEAGRASSES

To assess the total above ground production, carbon produced and turnover time for Orman Reefs seagrass meadows the information collected in the seagrass distribution and community structure surveys was combined with measurements of productivity for individual species and literature derived values of percent carbon for new growth (Figure 1). This information was used to estimate above ground production and meadow turnover for both the March and November sampling times.

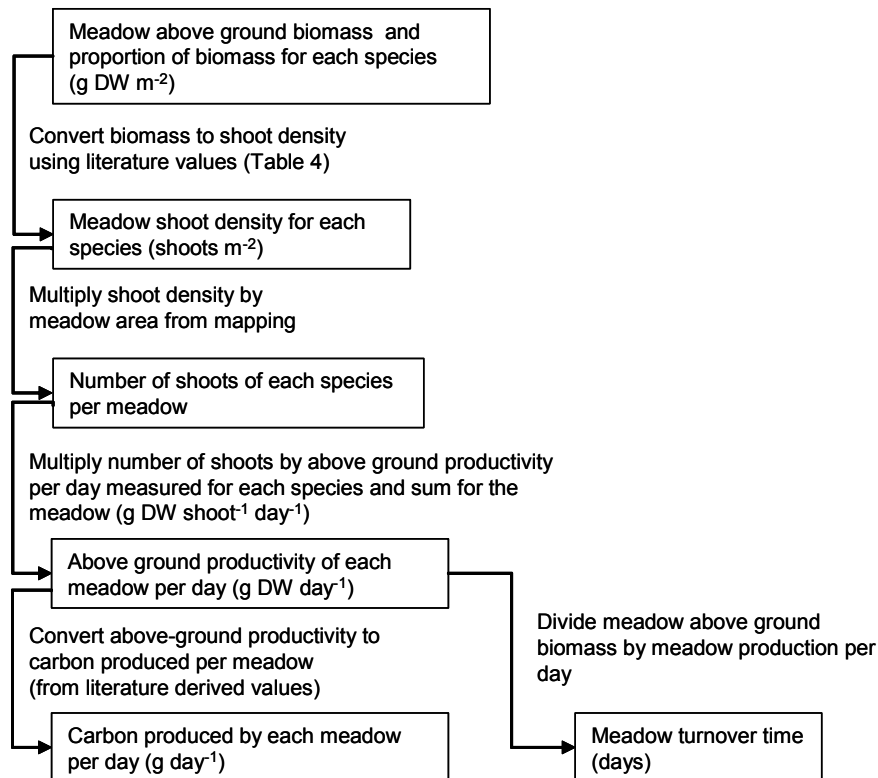


Figure 1. Flow chart detailing methodology for calculating above ground primary productivity, carbon produced and turnover time for seagrass meadows at Orman Reefs.

(A) Conversion of meadow above ground biomass to shoot density

The above ground biomass for seagrass meadows (measured in the surveys) was converted to meadow shoot densities for each species using values derived from other studies where both biomass and shoot density were recorded (Table 4). For the purposes of this study it was assumed that a linear relationship occurred between above ground biomass and shoot density for each of the species. Where possible values used were from studies that had been conducted in similar geographic locations during the same season. If more than one value was available the most conservative was used.

The calculated mean shoot densities for each species in each meadow (shoots m⁻²) were converted to number of shoots of each species per meadow by multiplying the shoot density

by the meadow area that was determined from the mapping surveys in March and November.

For the non-leaf replacing species found in the study area, *Halophila ovalis*, *H. decipiens*, and *H. spinulosa* the number of basal meristems (rhizome growing tips) in the meadows was also calculated. The ratio of basal meristems to shoots applied were obtained from previous studies of the species in nearby tropical locations (Table 4).

Table 4: A list of authors of studies from which shoot values were taken and applied to each of the species and meadows found at Orman Reefs.

Species	Shoot density to biomass ratio	Shoot density to basal meristem ratio	Study Location	Source
<i>C. rotundata</i>	1 : 0.040	N/A	Green Island, Qld, Australia	McKenzie (unpublished data)
<i>C. serrulata</i>	1 : 0.061	N/A	Port Moresby, Papua New Guinea	Brouns (1987)
<i>E. acoroides</i>	1 : 0.643	N/A	South Sulawesi, Indonesia	Eftemeijer (1994)
<i>H. decipiens</i>	1 : 0.002	1 : 0.333	St. Croix, US Virgin Islands	Kenworthy <i>et al.</i> (1989)
<i>H. ovalis</i>	1 : 0.003	1 : 0.245	Green Island, Qld, Australia and South Sulawesi, Indonesia	McKenzie (unpublished data) and Eftemeijer and Stapel (1999)
<i>H. spinulosa</i>	1 : 0.027	1 : 0.456	Moreton Bay, Qld, Australia and Harvey Bay, Qld, Australia	Knowles (2005) and Bité (unpublished data)
<i>H. uninervis</i>	1 : 0.004	N/A	Green Island, Qld, Australia	McKenzie (unpublished data)
<i>S. isoetifolium</i>	1 : 0.010	N/A	Port Moresby, Papua New Guinea	Brouns (1987)
<i>T. ciliatum</i>	1 : 0.105	N/A	Inhaca Island, Mozambique	Bandeira (2002)
<i>T. hemprichii</i>	1 : 0.020	N/A	Green Island, Qld, Australia	McKenzie (unpublished data)

(B) Above ground production of species

In March and November 2004, above ground productivity information for each species found in the Orman Reefs meadows was collected from Anui Reef and Thursday Island, both situated in the Torres Strait. Anui Reef forms part of the Orman Reefs and Thursday Island is situated towards the southern end of the Torres Strait (see Map 1). These two locations were chosen based on their diverse assembly of seagrass and proximity to the study site. Logistical issues prevented the collection of *in situ* productivity measurements for two of the minor species found in the study, *Syringodium isoetifolium* and *Halophila decipiens*. For these two species values collected from previous studies in tropical locations were used (Brouns 1987; Kenworthy *et al.* 1989). The methods outlined in Short and Duarte (2001) were used to determine the above ground productivity of species. Three methods were used according to the growth habits of the species found in the survey:

(i) Leaf marking

For leaf replacing seagrass species the leaf growth rate was determined using the *in situ* leaf marking method (Short and Duarte 2001). A hole was punched through all the leaves of an individual shoot using a syringe just below the top of the basal meristem (sheath) of each

shoot (Plate 3). As a leaf grew, the pinhole scar from needle punching moved upwards from the basal meristem. The new leaf growth was any growth that occurred between the hole in the sheath and the scar on the leaf. Old growth was that which occurred before marking (between the pinhole scar on the leaf and the leaf tip). A minimum of 30 shoots were marked for each species.

Plants were harvested 3 to 8 days after marking and brought back to the laboratory for separation into old and new growth. Samples were washed in freshwater to remove salt and any epiphytes scraped off. The area of old and new parts of the leaf were measured using a leaf scanner (mm^2). Dry weight was then obtained by separating new and old growth (Plate 4) and drying them in an oven at a constant temperature of 60°C for 48 hours. In order to reduce the error associated with weighing very small and light sections of individual leaves, the samples for each species were pooled and the old and new leaf components were weighed. We then calculated the dry weight per unit of leaf area by dividing the pooled weight by the surface area of leaves obtained from the scanner. The dry weight biomass of each leaf section was then calculated by multiplying the measured surface area of each leaf section by the weight per unit area.



Plate 3 Diver marking seagrass tissue with syringe



Plate 4 New" and "old" biomass samples ready to be measured and dried

(ii) Rhizome tagging

For non-leaf replacing species such as *Halophila ovalis* the rhizome tagging method described by Short and Duarte (2001) was used. Rhizomes were tagged at the basal meristem with a coloured wire loop. Subsequent growth of the tagged seagrass produced a new shoot and roots that trapped the wire loop in the newly formed node. Tagged seagrasses were harvested 3 to 8 days after tagging and biomass of new leaf material was measured in the laboratory and expressed as biomass added per day in g DW m^{-2} . A minimum of 5 rhizomes were tagged for each species.

(iii) Leaf clipping

For the di-meristematic non-leaf replacing species, *Halophila spinulosa*, a leaf clipping method (Short and Duarte 2001) was used in addition to rhizome tagging. This species has a meristem at the tip of the leaf cluster where new leaves are produced on existing shoots as well as the new leaf shoots produced at the basal meristem on the rhizome. The youngest leaf on the tip of 56 individual shoots was clipped in the field at a "radical" angle that could be recognised when the plants were harvested 4 days after clipping. New growth added was

determined by removing drying and weighing any leaves that were produced above the “clipped” leaf on the shoot.

(C) Above ground productivity of meadows

To calculate the total above ground productivity of meadows the number of shoots (leaf replacing species) or basal meristems (non-leaf replacing) of each species in the meadow (see section A above) was multiplied by the biomass added for each shoot or basal meristem per day calculated in section B above). Meadow above ground productivity was expressed as dry weight added for each meadow per day (g DW day^{-1}) and was calculated for both the March and November sampling times.

(D) Meadow turnover

The turnover time of each meadow was measured by dividing the meadow biomass (g DW m^{-2}) by the meadow productivity (section C) ($\text{g DW m}^{-2} \text{ day}^{-1}$). The resulting figure represents the number of days required for a meadow to completely turnover its current standing above ground biomass.

(E) Above ground carbon production

For this study a value of 34.34% of the total above ground dry weight produced by seagrasses as being comprised of carbon was used. This value was determined by taking the average values of carbon production for similar seagrass species to those found at Orman Reefs from a review of previous studies. including Atkinson and Smith (1983), Erftemeijer (1994), Koike (1987), Hemminga *et al.* (1995) and Lobb (unpublished data). These particular studies were utilised because of their similarity geographically and environmentally to our study site. Carbon productivity in these studies ranged from 29.0% to 40.4% of the dry weight biomass.

RESULTS

1. SEAGRASS DISTRIBUTION AND COMMUNITY STRUCTURE

Seagrass species

Ten seagrass species (from two families) were identified in the meadows on Orman Reefs:

Family CYMODOCEACEAE Taylor:



Cymodocea rotundata
Ehrenb. Et Hempr. Ex Aschers



Cymodocea serrulata
(R.Br.) Aschers. and Magnus



Halodule uninervis
(wide and narrow leaf morphology)
(Forsk.) Aschers. in Boissier



Syringodium isoetifolium
(Aschers.) Dandy

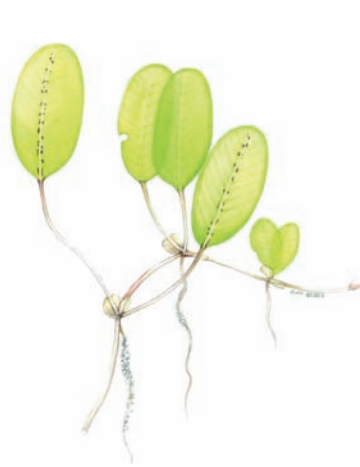


Thalassodendron ciliatum
(Forsk.) den Hartog

Family HYDROCHARITACEAE Jussieu:



Thalassia hemprichii
(Ehrenb.) Aschers. in Petermann



Halophila ovalis
(R. Br.) Hook. F.



Halophila spinulosa
(R. Br.) Aschers. In Neumayer

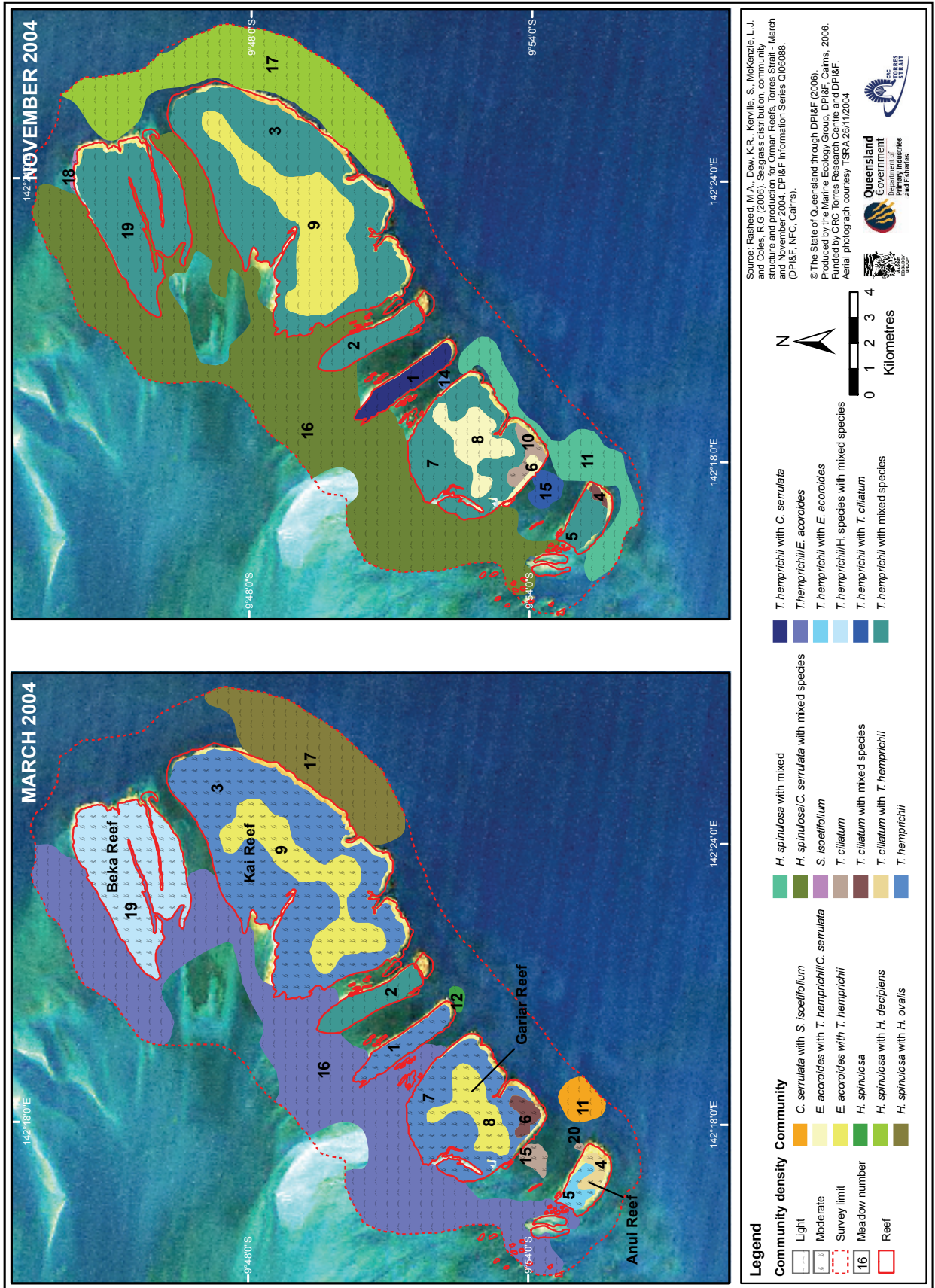


Halophila decipiens
Ostenfeld



Enhalus acoroides
(L.F.) Royle

Map 2. Seagrass distribution and community types at Orman Reefs in March and November 2004



Seagrass distribution and abundance for the Orman Reefs meadows

An extensive seagrass coverage was found within the Orman Reefs survey area in both March and November 2004 (Map 2). Seagrass covered the majority of the intertidal reef top areas and a large proportion of the subtidal areas examined in the surveys. There were marked differences in seagrass above ground biomass, distribution and species composition between the two surveys.

March 2004

A total of 333 ground truth sites were surveyed at Orman Reefs during March 2004 with 52% of sites having seagrass present. Of these 247 sites were surveyed from boat (62 sites using camera and 185 sites using divers) and 86 intertidal sites were surveyed from helicopter.

The 16 seagrass meadows mapped were mostly on intertidal reef tops. The 10 individual intertidal meadows, had moderate above ground biomass and were dominated by the larger seagrass species *T. hemprichii* and *E. acoroides* (Map 2, 3; Table 5). The subtidal meadows were lower in biomass and were composed of varying community types, however the smaller *Halophila* species generally dominated these meadows (Maps 2, 3; Table 5).

The total area mapped in the 16 meadows was $18,683.9 \pm 4,837$ ha. The intertidal reef tops were almost completely covered by seagrass with 9,491.2 ha mapped in intertidal regions (Maps 2, 3; Table 5). Meadow areas ranged from 10.3 ha at meadow 20, situated on outer Anui Reef, to 6,905.5 ha for meadow 16, located subtidally to the north of Orman Reefs (Maps 2, 3; Table 5). Subtidal seagrass distribution in the region was likely to be more extensive than that mapped as many meadows extended beyond the survey limit (greater than 1 nm from the reef edge).

Above ground biomass was greater in intertidal meadows than subtidal meadows. The 10 intertidal meadows had a mean above ground biomass of 31.8 g DW m^{-2} . The biomass of individual meadows however ranged from 10.4 g DW m^{-2} to $99.35 \text{ g DW m}^{-2}$ (Table 5). Subtidal meadows had lower above ground biomass (13.1 g DW m^{-2}) ranging from 0.01 g DW m^{-2} in meadow 11 to 52.6 g DW m^{-2} in meadow 15. Intertidal and subtidal meadows with higher biomass were dominated by the larger species of *T. hemprichii*, *T. ciliatum* and *E. acoroides* whereas meadows with lower biomass were largely dominated by *H. spinulosa*.

November 2004

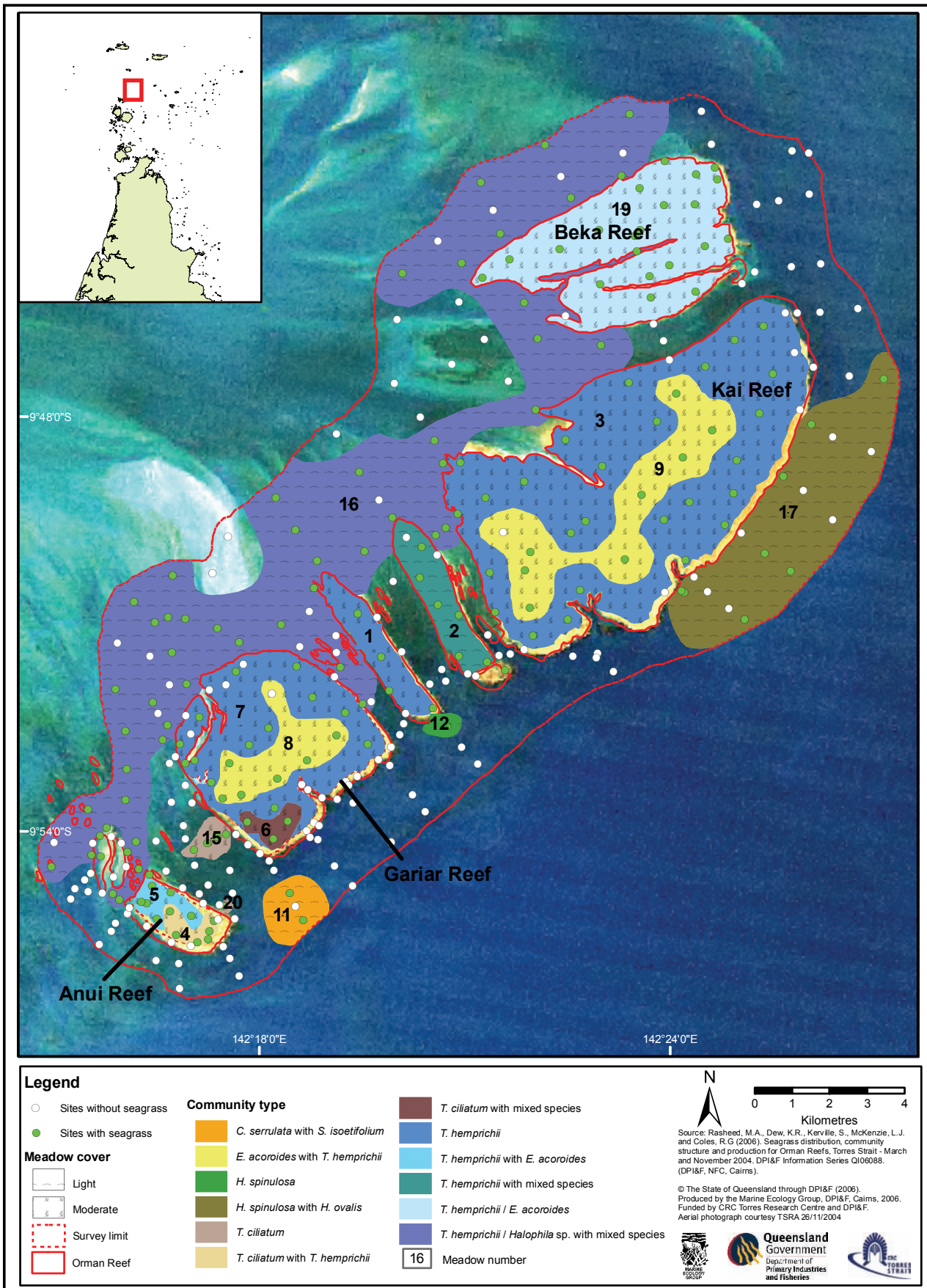
Seagrass was present at 279 (67%) of the 418 survey sites (Map 4; Table 6). These sites included 143 sites viewed from helicopter, 103 using a real-time video camera and 172 using free divers.

The 17 meadows that were mapped included 12 different community types based on species presence and dominance (Map 2, 4; Table 6). Similar to the results in March, the 10 intertidal meadows covered the majority of the reef top area (9,456.7 ha) but were classified as having only a light biomass typically dominated by *T. hemprichii*. The only meadow in the November survey to be classified as having a moderate biomass was a *T. ciliatum* dominated meadow on Gariar Reef (Meadow 6). The area of subtidal seagrass had increased in November to 12,144.8 ha (32% increase) largely due to the expansion of meadows 11 and 17 off the deeper south-western edge of the reefs (Maps 2 & 4; Figure 2). Subtidal meadows were again typically light in biomass and dominated by *H. spinulosa* (Map 2, 4; Table 6).

The total above ground biomass varied greatly between individual meadows according to the dominant species present. In November both intertidal and subtidal meadows had declined substantially in biomass since the March survey with a 70% reduction for intertidal (mean of 9.6 g DW m⁻²) and 66% reduction for sub-tidal meadows (mean 4.5 g DW m⁻²) (Tables 5 & 6). Of the 14 seagrass meadows that were present in both surveys ten meadows recorded a reduction in above ground biomass of more than 50% between March and November (Figure 2). The reduction in meadow biomass was more substantial in intertidal than subtidal meadows. In subtidal areas the reduction in mean meadow biomass was linked to a substantial increase in meadow area of low biomass *Halophila* species (Maps 3 & 4; Tables 5 & 6).

The species composition of intertidal meadows was generally similar between March and November surveys although *C. serrulata* appeared to be less affected by the large declines in meadow biomass than other species (Tables 5 & 6; Figure 2). Intertidal meadows were still dominated by *E. acoroides* and *T. hemprichii* but *C. serrulata* generally made up a larger proportion of the above ground biomass in November than in March. In subtidal areas there was an increase in *H. spinulosa* in November. The majority of the increased area of subtidal seagrass was due to the expansion of *H. spinulosa* in meadows 11 and 17 in the deep waters to the east of Orman Reefs (Maps 3 & 4; Figure 2).

Map 3. Seagrass distribution and community types for Orman Reefs in March 2004



Map 4. Seagrass distribution and community types for Orman Reefs in November 2004

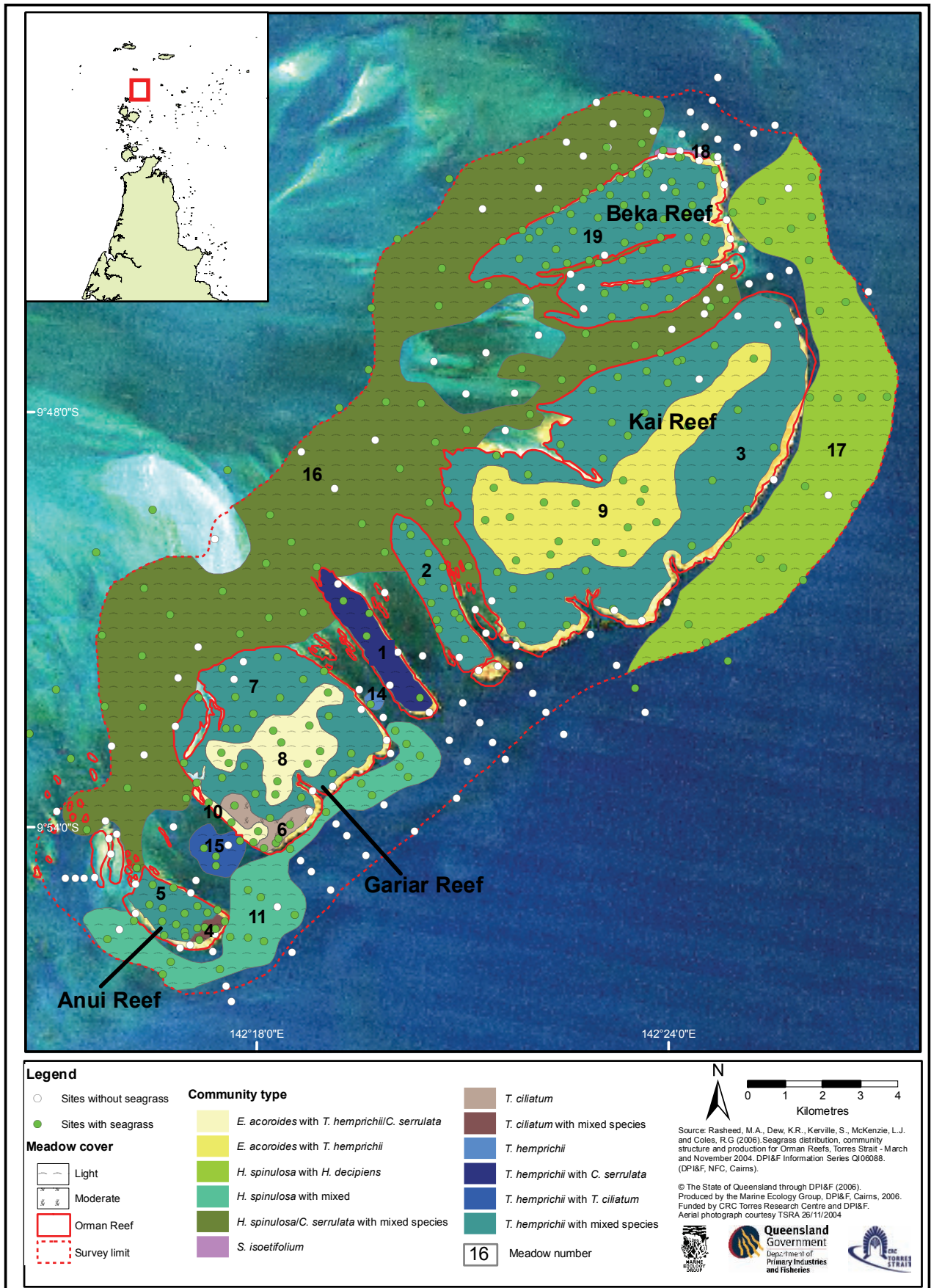


Table 5. A summary of the distribution, abundance and productivity of seagrass meadows at Orman Reefs in March 2004

Meadow Number (see map3)	Distribution and Abundance					Productivity				
	Species present (% composition of biomass)	No. of sites	Mean above ground biomass (g DW m ⁻²)	Area ± R (ha)	Total meadow above ground production (t DW meadow day ⁻¹)	Mean above ground production (g DW m ⁻² day ⁻¹)	Total meadow carbon production (t meadow day ⁻¹)	Mean carbon production (g m ⁻² day ⁻¹)	Meadow turnover (days)	
1	<i>T. hemprichii</i> (65), <i>C. serrulata</i> (28), <i>H. ovalis</i> (7)	6	3.11 ± 0.89	322.64 ± 110.64	0.854	0.265	0.294	0.091	12.005	
2	<i>T. hemprichii</i> (71), <i>C. serrulata</i> (12), <i>H. spinulosa</i> (6), <i>C. rotundata</i> (5), <i>H. ovalis</i> (2), <i>T. ciliatum</i> (4)	13	7.50 ± 1.61	389.92 ± 106.84	2.694	0.691	0.927	0.238	7.455	
3	<i>T. hemprichii</i> (86), <i>C. serrulata</i> (9), <i>E. acoroides</i> (2), <i>C. rotundata</i> (2), <i>H. ovalis</i> (1)	31	7.49 ± 1.85	3232.85 ± 633.85	22.640	0.700	7.787	0.241	10.766	
4	<i>T. ciliatum</i> (86), <i>T. hemprichii</i> (6), <i>E. acoroides</i> (3), <i>S. isoetifolium</i> (3), <i>C. serrulata</i> (2)	4	33.82 ± 6.73	32.79 ± 30.66	1.038	3.167	0.357	1.089	10.692	
5	<i>E. acoroides</i> (43), <i>T. hemprichii</i> (34), <i>C. serrulata</i> (10), <i>T. ciliatum</i> (9), <i>H. ovalis</i> (2), <i>C. rotundata</i> (2)	14	5.74 ± 2.93	243.04 ± 71.02	0.820	0.337	0.282	0.116	17.211	
6	<i>T. ciliatum</i> (92), <i>E. acoroides</i> (3), <i>T. hemprichii</i> (3), <i>S. isoetifolium</i> (1), <i>H. ovalis</i> (1)	6	46.24 ± 4.28	136.8 ± 78.49	6.069	4.436	2.087	1.526	10.423	
7	<i>T. hemprichii</i> (70), <i>C. serrulata</i> (17), <i>C. rotundata</i> (6), <i>H. ovalis</i> (6)	23	3.47 ± 0.92	1197.46 ± 359.59	3.784	0.316	1.301	0.109	11.119	
8	<i>E. acoroides</i> (64), <i>T. hemprichii</i> (20), <i>C. serrulata</i> (17), <i>C. rotundata</i> (6), <i>H. ovalis</i> (1)	10	13.11 ± 5.90	474.13 ± 138.06	2.364	0.499	0.813	0.171	26.927	
9	<i>E. acoroides</i> (43), <i>T. hemprichii</i> (42), <i>C. serrulata</i> (6), <i>T. ciliatum</i> (5), <i>C. rotundata</i> (3), <i>H. ovalis</i> (1), <i>H. uninervis</i> (<1)	17	19.69 ± 5.48	1607.26 ± 243.85	19.159	1.192	6.590	0.410	16.645	
10	<i>E. acoroides</i> (56), <i>T. hemprichii</i> (23), <i>C. serrulata</i> (17), <i>C. rotundata</i> (3), <i>H. ovalis</i> (2)	5	10.60 ± 6.12	71.21 ± 30.95	0.323	0.454	0.111	0.156	23.998	
19	<i>T. hemprichii</i> (72), <i>C. serrulata</i> (12), <i>E. acoroides</i> (10), <i>H. ovalis</i> (5), <i>C. rotundata</i> (1), <i>H. uninervis</i> (<1)	57	6.09 ± 2.43	1748.58 ± 293.39	9.294	0.532	3.197	0.183	11.617	
Sub-total		186	9.61 ± 0.87	9456.68 ± 2097.34	69.039	1.144	23.746	0.39		
11	<i>H. spinulosa</i> (88), <i>H. decipiens</i> (9), <i>C. serrulata</i> (1), <i>T. hemprichii</i> (1), <i>S. isoetifolium</i> (1), <i>H. ovalis</i> (<1)	17	2.08 ± 1.11	1208.94 ± 300.03	2.318	0.192	0.797	0.066	10.846	
14	<i>T. hemprichii</i> (100)	1	0.01	19.78 ± 8.77	0.000	<0.001	0.000	<0.001	8.475	
15	<i>T. hemprichii</i> (92), <i>T. ciliatum</i> (8)	5	6.28 ± 2.57	150.09 ± 107.85	0.959	0.639	0.330	0.220	9.827	
16	<i>H. spinulosa</i> (39), <i>C. serrulata</i> (26), <i>H. ovalis</i> (8), <i>T. hemprichii</i> (8), <i>S. isoetifolium</i> (11), <i>E. acoroides</i> (2), <i>H. uninervis</i> (2), <i>H. decipiens</i> (2), <i>C. rotundata</i> (1)	77	5.51 ± 1.04	7740.4 ± 2156.75	31.115	0.402	10.702	0.138	20.522	
17	<i>H. spinulosa</i> (89), <i>H. decipiens</i> (11), <i>T. hemprichii</i> (<1)	22	2.86 ± 1.32	3002.97 ± 749.73	7.977	0.266	2.744	0.091	10.766	
18	<i>S. isoetifolium</i> (92), <i>H. ovalis</i> (5), <i>C. serrulata</i> (3)	3	7.80 ± 0.03	22.65 ± 18.98	0.065	0.286	0.022	0.098	27.241	
Sub-total		125	4.46 ± 0.72	12144.83 ± 3342.11	42.436	0.357	14.596	0.12		
TOTAL		311	7.57 ± 1.63	21601.51 ± 5439.45	111.47	0.75	38.34	0.26		

Table 6. A summary of the distribution, abundance and productivity of seagrass meadows at Orman Reefs in November 2004

Meadow Number (see map3)	Distribution and Abundance					Productivity			
	Species present (% composition of biomass)	No. of sites	Mean above ground biomass (g DW m ⁻²)	Area ± R (ha)	Total meadow above ground production (t DW meadow day ⁻¹)	Mean above ground production (g DW m ⁻² day ⁻¹)	Total meadow carbon production (t meadow day ⁻¹)	Mean carbon production (g m ⁻² day ⁻¹)	Meadow turnover (days)
1	T. hemprichii (65), C. serrulata (28), H. ovalis (7)	6	3.11 ± 0.89	322.64 ± 110.64	0.854	0.265	0.294	0.091	12.005
2	T. hemprichii (71), C. serrulata (12), H. spinulosa (6), C. rotundata (5), H. ovalis (2), T. ciliatum (4)	13	7.50 ± 1.61	389.92 ± 106.84	2.694	0.691	0.927	0.238	7.455
3	T. hemprichii (86), C. serrulata (9), E. acoroides (2), C. rotundata (2), H. ovalis (1)	31	7.49 ± 1.85	3232.85 ± 633.85	22.640	0.700	7.787	0.241	10.766
4	T. ciliatum (86), T. hemprichii (6), E. acoroides (3), S. isoetifolium (3), C. serrulata (2)	4	33.82 ± 6.73	32.79 ± 30.66	1.038	3.167	0.357	1.089	10.692
5	E. acoroides (43), T. hemprichii (34), C. serrulata (10), T. ciliatum (9), H. ovalis (2), C. rotundata (2)	14	5.74 ± 2.93	243.04 ± 71.02	0.820	0.337	0.282	0.116	17.211
6	T. ciliatum (92), E. acoroides (3), T. hemprichii (3), S. isoetifolium (1), H. ovalis (1)	6	46.24 ± 4.28	136.8 ± 78.49	6.069	4.436	2.087	1.526	10.423
7	T. hemprichii (70), C. serrulata (17), C. rotundata (6), H. ovalis (6)	23	3.47 ± 0.92	1197.46 ± 359.59	3.784	0.316	1.301	0.109	11.119
8	E. acoroides (64), T. hemprichii (20), C. serrulata (17), C. rotundata (6), H. ovalis (1)	10	13.11 ± 5.90	474.13 ± 138.06	2.364	0.499	0.813	0.171	26.927
9	E. acoroides (43), T. hemprichii (42), C. serrulata (6), T. ciliatum (5), C. rotundata (3), H. ovalis (1), H. uninervis (<1)	17	19.69 ± 5.48	1607.26 ± 243.85	19.159	1.192	6.590	0.410	16.645
10	E. acoroides (56), T. hemprichii (23), C. serrulata (17), C. rotundata (3), H. ovalis (2)	5	10.60 ± 6.12	71.21 ± 30.95	0.323	0.454	0.111	0.156	23.998
19	T. hemprichii (72), C. serrulata (12), E. acoroides (10), H. ovalis (5), C. rotundata (1), H. uninervis (<1)	57	6.09 ± 2.43	1748.58 ± 293.39	9.294	0.532	3.197	0.183	11.617
Sub-total		186	9.61 ± 0.87	9456.68 ± 2097.34	69.039	1.144	23.746	0.39	
11	H. spinulosa (88), H. decipiens (9), C. serrulata (1), T. hemprichii (1), S. isoetifolium (1), H. ovalis (<1)	17	2.08 ± 1.11	1208.94 ± 300.03	2.318	0.192	0.797	0.066	10.846
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16	H. spinulosa (39), C. serrulata (26), H. ovalis (8), T. hemprichii (8), S. isoetifolium (11), E. acoroides (2), H. uninervis (2), H. decipiens (2), C. rotundata (1)	77	5.51 ± 1.04	7740.4 ± 2156.75	31.115	0.402	10.702	0.138	20.522
17	H. spinulosa (89), H. decipiens (11), T. hemprichii (<1)	22	2.86 ± 1.32	3002.97 ± 749.73	7.977	0.266	2.744	0.091	10.766
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Sub-total		125	4.46 ± 0.72	12144.83 ± 3342.11	42.436	0.357	14.596	0.12	
TOTAL		311	7.57 ± 1.63	21601.51 ± 5439.45	111.47	0.75	38.34	0.26	

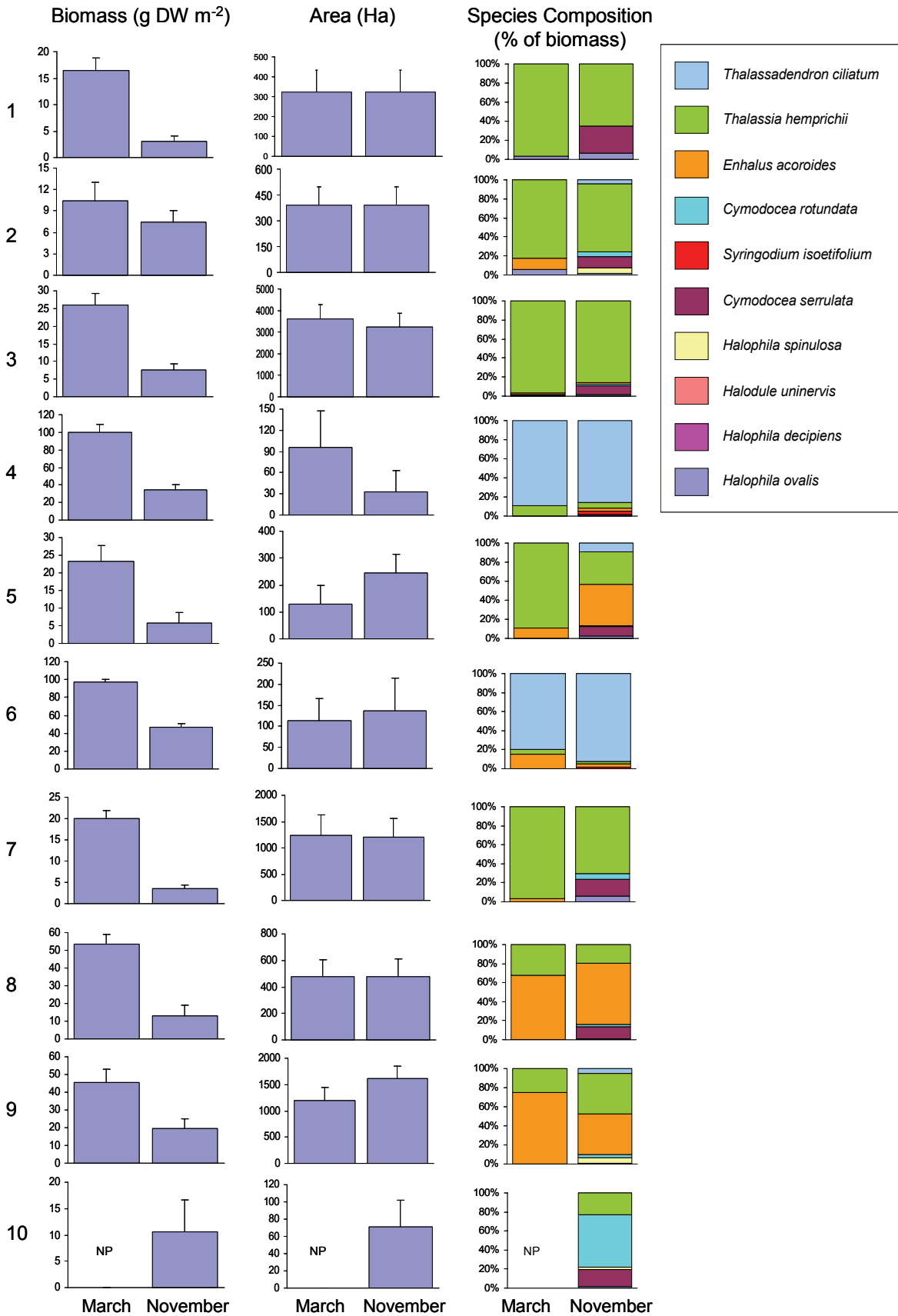


Figure 2a Biomass, area and species composition of Orman Reefs seagrass meadows (1-10) in March and November 2004.

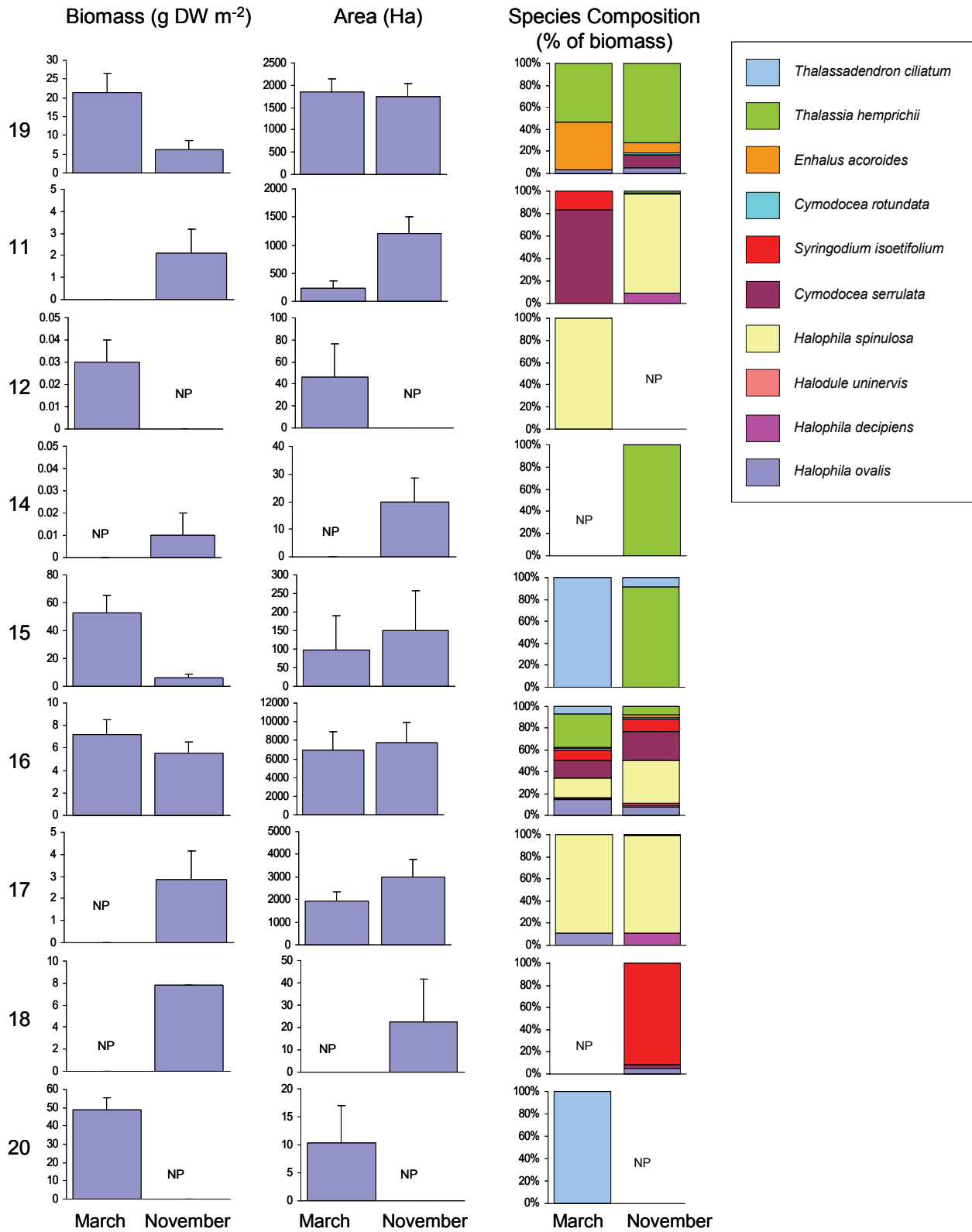


Figure 2b Biomass, area and species composition of Orman Reefs seagrass meadows (11-20) in March and November 2004

2. ABOVE GROUND PRODUCTIVITY OF ORMAN REEFS SEAGRASSES

Above ground production of seagrass species

Seagrass net above ground productivity varied markedly between species (Table 7). Differences generally varied according to shoot size differences between species with the largest species adding the greatest biomass per shoot per day. The two largest species, *Enhalus acoroides* and *Thalassodendron ciliatum* added the greatest dry weight per shoot per day (0.0273 and 0.0105 g DW shoot⁻¹ day⁻¹ respectively) and were an order of magnitude higher than *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata* and *Halophila spinulosa* (Table 7). The smallest *Halophila* and *Halodule* species added the least amount of biomass with *Halodule uninervis* having the lowest productivity per shoot of any species (4.1×10^{-4} g DW shoot⁻¹ day⁻¹).

Table 7. Rate of new growth per shoot (g) used to determine productivity and turnover time of seagrass meadows at Orman Reefs in March and November, 2004.

Species	Marking technique used	New growth g DW shoot day ⁻¹	Source
<i>Cymodocea rotundata</i>	leaf marking	0.002900	<i>This study</i>
<i>Cymodocea serrulata</i>	leaf marking	0.001600	<i>This study</i>
<i>Enhalus acoroides</i>	leaf marking	0.027300	<i>This study</i>
<i>Halophila decipiens</i>	rhizome tagging	0.000625	Kenworthy <i>et al.</i> (1989)
<i>Halophila ovalis</i>	rhizome tagging	0.000500	<i>This study</i>
<i>Halophila spinulosa</i> - basal meristem	rhizome tagging	0.003063	<i>This study</i>
<i>Halophila spinulosa</i> - leaf meristem	leaf clipping	0.001142	<i>This study</i>
<i>Halodule uninervis</i>	leaf marking	0.00041	<i>This study</i>
<i>Syringodium isoetifolium</i>	leaf marking	0.000319	Brouns (1987)
<i>Thalassodendron ciliatum</i>	leaf marking	0.010488	<i>This study</i>
<i>Thalassia hemprichii</i>	leaf marking	0.004261	<i>This study</i>

Above ground productivity of meadows

The Orman Reefs seagrass meadows had a total net above ground productivity of 259.81 t DW day⁻¹ in March and a substantially lower 111.47 t DW day⁻¹ in November (Tables 5 & 6). The majority of this production came from the intertidal meadows which accounted for 81% of the total production in March and 63% in November. The large intertidal meadows on Beka, Kai and Gariar Reefs (meadows 3, 7, 9 and 19; Maps 3 & 4) and the large subtidal meadow to the west of Orman Reefs (meadow 16) accounted for the majority of the above ground productivity in both surveys (Maps 1 & 2; Tables 5 & 6).

Meadows that were dominated by *Thalassodendron ciliatum* had the greatest productivity per square metre (from 4.9 to 9.9 g DW m⁻² day⁻¹ in March and 3.1 to 4.4 g DW m⁻² day⁻¹ in November) but due to their relatively small size added only a minor component to the total above ground production at Orman Reefs (Tables 5 & 6). The large meadows that provided the majority of the above ground production had much lower production per unit area (from 0.6 to 2.6 g DW m⁻² day⁻¹ in March and 0.4 to 1.2 g DW m⁻² day⁻¹ in November). These meadows were dominated by species with lower production per shoot such as *Thalassia hemprichii* and had lower biomass and shoot densities than the *Thalassodendron ciliatum* meadows (Tables 5 & 6).

While there was an overall reduction in both intertidal and subtidal meadow production between March and November the two subtidal meadows dominated by *Halophila spinulosa* (meadows 11 and 17) went against the trend with an increase in production per unit area and total meadow production. Unlike the majority of seagrass meadows these meadows located off the deeper eastern edge of Orman Reefs had increased in biomass, shoot density and area between surveys.

Meadow turnover

The time required for meadows to turn over their above ground biomass ranged from 9.6 to 26.8 days in March and 8.5 to 27.2 days in November (Tables 5 & 6). The majority of both intertidal and subtidal meadows could completely turn over their standing crop in approximately 10 days (Tables 5 & 6). The turnover time for meadows reflected their species composition with meadows dominated by species with long turnover times taking longer to turn over than those dominated by species with short turnover times (Figure 3). Meadows that were dominated by *Enhalus acoroides* had the longest turnover time in both surveys (22.4 to 25.7 days in March and 23.4 to 26.3 days in November). The biggest change in turnover time between surveys was for the subtidal meadow 11 which had a reduction in turnover time from 26.8 days in March to 10.9 days in November (Tables 5 & 6). The reduced turnover time for this meadow was accompanied by a shift in species composition between surveys from the slower growing *Cymodocea serrulata* and *Syringodium isoetifolium* to the faster *Halophila spinulosa* (Figure 3; Tables 5 & 6).

Above ground carbon production

The Orman Reefs seagrass meadows incorporated a total of 89.4 tonnes of carbon per day in March and 38.0 tonnes in November into their above ground biomass (Tables 5 & 6). As with the overall above ground productivity the majority of carbon was added by the intertidal meadows in both surveys (Tables 5 & 6). The rate of carbon production per unit area was 1.19 g C m⁻² day⁻¹ (1.15 intertidal and 1.23 subtidal) in March and 0.26 g m⁻² day⁻¹ (0.39 intertidal and 0.12 subtidal) in November.

Mean carbon production varied considerably between meadows from <0.001 to 3.41 g C m⁻² day⁻¹ in March (Table 5) and <0.001 to 1.53 g C m⁻² day⁻¹ in November (Table 6). Meadows dominated by species that added the greatest biomass per day, such as *Thalassodendron ciliatum* and *Enhalus acoroides*, had the greatest rate of carbon production per unit area. However, these meadows formed only a minor component of the total carbon incorporated by Orman Reefs seagrasses due to their relatively small size (Tables 5 & 6). The same large meadows that were responsible for the majority of the total above ground production also incorporated the most amount of carbon (meadows 3, 6, 9 & 19; Tables 5 & 6).

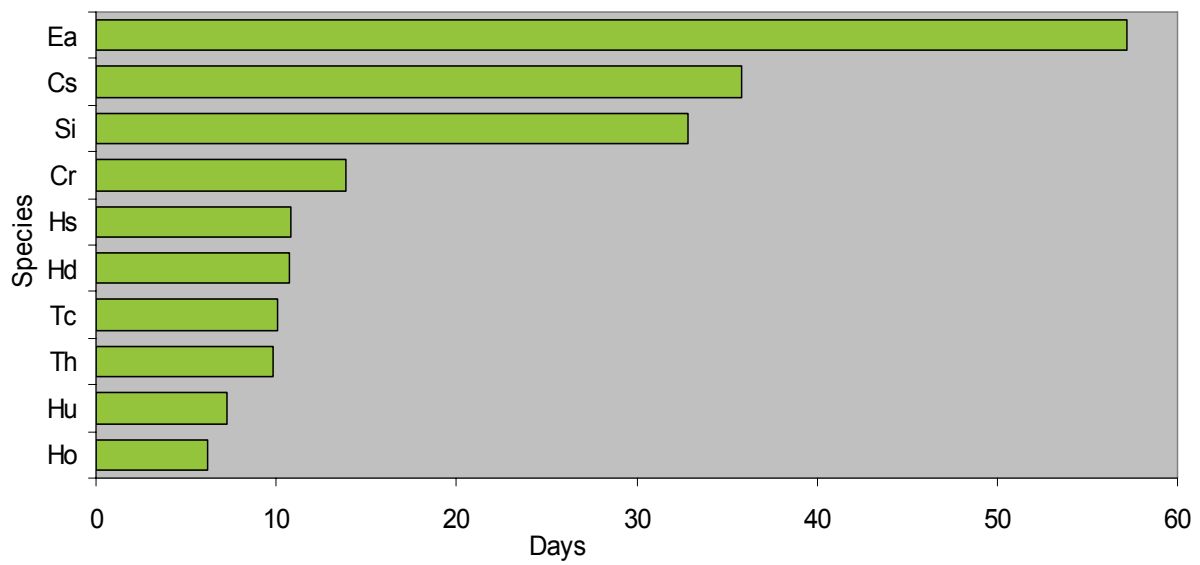


Figure 3. Above ground turnover time for Orman Reefs seagrass species. Ea = *Enhalus acoroides*; Cs = *Cymodocea serrulata*; Si = *Syringodium isoetifolium*; Cr = *Cymodocea rotundata*; Hs = *Halophila spinulosa*; Hd = *Halophila decipiens*; Tc = *Thalassodendron ciliatum*; Th = *Thalassia hemprichii*; Hu = *Halodule uninervis*; Ho = *Halophila ovalis*.

DISCUSSION

This study describes in detail the seagrass distribution, abundance and community structure of a large tropical reef platform seagrass community in the Torres Strait and uses this information to provide an estimate of the above ground-productivity and carbon assimilated by the seagrass meadows. The approach used here is one of the first to attempt this on a large scale utilising detailed seagrass community information collected in the field. We were able to demonstrate a marked change in seagrass biomass, distribution, species composition, productivity and carbon assimilated between the two seasonal surveys. The 21,600ha of seagrass mapped in the surveys is likely to be a significant resource to the region and is one of the largest areas of shallow seagrasses described in northern Australia.

The diversity of seagrass species at Orman Reefs was high, with ten of the twelve known species to occur in Torres Strait observed (Bridges *et al.* 1982). Patterns of seagrass distribution and community structure were typical of those found in neighbouring Papua New Guinea (Brouns 1987) and other Indo-Pacific countries (Erftemeijer and Herman 1994; Fokeera-Wahedally and Bhikajee 2005). Intertidal areas in the region are commonly dominated by the larger growing species such as *T. ciliatum*, *T. hemprichii* and *E. acoroides* (Bridges *et al.* 1982) with the smaller *H. spinulosa*, *H. decipiens* and *H. ovalis* being more common in deeper subtidal areas (Coles *et al.* 2000).

The large within-year changes in seagrass distribution, species composition and biomass recorded for Orman Reefs reflected the seasonal variation that has been recorded at other nearby locations such as in the Gulf of Carpentaria (Rasheed *et al.* 2001) and Cape York (Roelofs *et al.* 2003). In these regions above ground biomass and distribution of intertidal meadows tends to be greatest in the period following the summer months and wet season (between March and June). The magnitude of biomass change we recorded was high for tropical seagrass meadows, which have in the past been assumed to be relatively stable, compared to temperate seagrasses (Zieman 1987). These early studies on tropical seagrass seasonality were focused in the Caribbean where environmental conditions are relatively stable and the tidal range is small (Zieman 1987). However in the Indo-Pacific the tidal range is much greater and has been shown to have a major influence on structuring seasonal changes in intertidal seagrass communities (Erftemeijer and Herman 1994).

At Orman Reefs it was likely that tidal exposure of intertidal meadows was a major influence in structuring the observed changes between March and November. Daytime tides at Orman Reefs were substantially lower between August and December than earlier in the year, resulting in increased daytime exposure of the meadows prior to the November survey (Figure 4). This increased exposure also occurred at a time of year when daily maximum temperatures were reaching their annual peak (Bureau of Meteorology 2006; Figure 5 & 6). The influence of high temperatures and exposure related desiccation has resulted in die-back of above ground biomass and a decrease in photosynthetic rate for seagrasses (Bulthuis and Woelkerling 1983; Kerr and Strother 1989; McKenzie 1994). Similar tidal exposure of *T. hemprichii* and *E. acoroides* meadows in Barang Lompo, Indonesia resulted in significant declines in above ground biomass through desiccation and "burning" of leaves (Erftemeijer and Herman 1994) and declines of intertidal *E. acoroides* meadows in Weipa approximately 250 km south of the Torres Strait were also linked to exposure related desiccation (Roelofs *et al.* 2003). Other studies in tropical Queensland have found that even in areas where seagrasses are protected from desiccation by shallow pools of water at low tide, water temperatures can reach levels that inhibit photosynthesis and lead to tissue death (Campbell *et al.* 2006).

The seagrass declines observed from March to November for intertidal areas did not occur for all of the subtidal meadows. Many subtidal meadows had expanded in area between the two surveys with meadows dominated by *H. spinulosa* also increasing in biomass. As the subtidal meadows were not exposed at low tide they would have been protected from desiccation and any extremes of temperature that may have been experienced in neighbouring intertidal meadows. Similar differences between subtidal and intertidal seagrass meadows have been recorded elsewhere in tropical Queensland where unseasonably high temperatures associated with drought and exposure have led to declines in intertidal meadows but increases in subtidal meadows (Rasheed *et al.* 2005; 2006). The increased abundance of *H. spinulosa* in November was typical for *Halophila* species growing in deeper water in tropical Australia. *Halophila tricostata* can be annual in Queensland only appearing late in the year (Kuo *et al.* 1993) and studies in three regions of the east coast of Queensland have found *H. spinulosa* to be far more abundant in October than May (Coles *et al.* 2002).

Above ground productivity and carbon assimilated by Orman Reefs seagrass meadows were a function of species composition, shoot density and size of seagrass meadows. Seasonal changes had a strong influence on all three of these factors and consequently had a strong effect on the total above ground production (259.8 t DW day⁻¹ in March and 111.5 t DW day⁻¹ in November) and carbon incorporated (89.4 t C day⁻¹ March and 38.0 t C day⁻¹ November) by Orman Reefs meadows. As intertidal meadows generally had higher shoot densities and covered a greater area they also contributed the majority of the production. However subtidal meadows had an increased contribution to overall productivity in November (from 19% to 38% of total) due to their expansion in both area and biomass (shoot density). Meadows dominated by the most productive species did not necessarily have the highest meadow productivity as they were either small in size (*T. ciliatum*) or had low shoot densities (*E. acoroides*). It was the large reef top meadows dominated by *T. hemprichii* that made the greatest contribution to overall productivity and carbon incorporated. Also, due to its large area, the subtidal meadow to the west of Orman Reefs made a significant contribution to overall productivity (17% in March and 28% in November) despite having a low productivity per unit area.

The above ground growth rates we measured for species at Orman Reefs were generally within the range of values recorded for the same species in other tropical locations. The leaf productivity rate for the most productive species in our study, *T. ciliatum* (0.0104 g DW shoot⁻¹ day⁻¹) was greater than that measured for an intertidal meadow in Kenya (0.006 g DW shoot⁻¹ day⁻¹; Uku and Björk 2005) but within the upper range recorded for the species growing in similar rocky and sandy substrates to Orman Reefs in Mozambique (0.0043 to 0.0106 g DW shoot⁻¹ day⁻¹; Bandeira 2000). The above ground productivity we measured for *H. ovalis*, *H. uninervis*, *S. isoetifolium*, *H. spinulosa* and *E. acoroides* were similar to other studies that have examined these species (Brouns and Heijs 1985; Knowles 2005; Longstaff *et al.* 1999; Udy *et al.* 1999; Vermaat *et al.* 1995).

Our study provides two “snapshots” of the above ground production and carbon assimilated by Orman Reefs seagrasses at times of year where there was most likely to be the greatest seasonal difference in seagrass abundance and thus productivity. However it was likely that the productivity and carbon assimilated would vary considerably around these two values. Seagrass meadow size and biomass are not constant and the rates of above ground production for seagrass species were likely to vary according to seasonal differences in the factors controlling seagrass growth (Duarte *et al.* 2006; Marbà *et al.* 1996; Moriarty *et al.* 1990; Uku and Björk 2005). *T. hemprichii*, for example, has been shown to have a large range in growth depending on the time of year (Uku and Björk 2005). However growth rates

of Orman Reefs seagrasses may not vary to the same extent, as the meadows were isolated from many of the terrestrial and anthropogenic influences such as nutrient runoff that were responsible for changes in seagrass productivity (Uku and Björk 2005). In the absence of anthropogenic and terrestrial influences the key factors controlling seagrass growth rates relate to seasonal changes in light and temperature (Duarte *et al.* 2006; Moriarty *et al.* 1990). Our measurements of seagrass growth were likely to be conservative as light and temperature conditions in the Torres Strait were less favourable in March (when measurements were taken) than in November. In March day length is shorter and wind and wave driven turbidity are higher than November (Swan 1981). Also average and maximum temperatures were lower in March than November (Bureau of Meteorology 2006).

The Orman Reefs seagrass meadows were highly productive when compared with other seagrass meadows that have been examined. The mean above ground production of seagrass meadows from our study in March was substantially higher than values recorded in a review by Duarte and Chiscano (1999) for meadows of the same species ($2.57 \text{ g DW m}^{-2} \text{ day}^{-1}$ compared with $1.58 \text{ g DW m}^{-2} \text{ day}^{-1}$). However In November, when intertidal meadows had declined in biomass and shoot density, the mean above ground production was lower ($0.75 \text{ g DW m}^{-2} \text{ day}^{-1}$). The high productivity at Orman Reefs was more remarkable given that the mean above ground biomass (and presumably shoot density) of the meadows in the Duarte and Chiscano (1999) review was substantially higher than for Orman Reefs meadows ($63.35 \text{ g DW m}^{-2}$ compared with $20.49 \text{ g DW m}^{-2}$ in March and 7.57 g DW m^{-2} in November) indicating that seagrass shoots were much more productive at Orman Reefs. This high productivity was most likely a reflection of the favourable conditions for seagrass growth that occur in the region, combined with very low levels of anthropogenic impact. Unlike the Orman Reefs study site, previous studies of tropical seagrass productivity have often been in locations where there are substantial terrestrial and anthropogenic impacts that had the potential to reduce seagrass productivity (e.g. Uku and Björk 2005; Vermaat *et al.* 1995).

Although not measured in this study below ground production was likely to add significantly to the total production and carbon assimilated by Orman Reefs seagrasses. Other studies have found that below ground production accounts for more than 32% of the total seagrass production (Duarte and Chiscano 1999) and this may be even higher when root production is included (up to 50 %, Duarte *et al.* 1998). A study in New Guinea found strong differences in the contribution to productivity made by below ground structures between many of the species that were also found at Orman Reefs ((17% for *T. hemprichii* 34% for *C. serrulata*, 50% for *C. rotundata* and 69% for *S. isoetifolium*) (Brouns 1987).

As well as having a high net primary productivity the meadows at Orman Reefs also had a rapid turnover time for their above ground biomass, with the majority of meadows able to replace their above ground biomass in 10 days. Meadow turnover time was a reflection of the species composition with meadows dominated by *Enhalus acoroides* having the longest turnover time. *E. acoroides* is typically a slow species to turnover its biomass taking up to 69 days in the Philippines (Estacion and Fortes 1988) and 57 days in our study. The slow turnover for *E. acoroides* was offset in the mixed species meadows at Orman Reefs due to the presence of faster turnover species within the meadows such as *T. hemprichii*, *H. ovalis* and *C. rotundata*. This resulted in the slowest meadow turnover being only 27 days.

Orman Reefs seagrass meadows also had a relatively high net carbon productivity (mean of $1.19 \text{ g C m}^{-2} \text{ day}^{-1}$ in March and $0.26 \text{ g C m}^{-2} \text{ day}^{-1}$ in November) when compared with other tropical seagrass meadows that have been studied (e.g. Lindeboom and Sandee 1989; Kenworthy *et al.* 1989; Moriarty 1990). Erftemeijer and Stapel (1999) recorded net primary

productivity for *H. ovalis* meadows of between 0.83 and 1.38 g C m⁻² day⁻¹ but 34% of this was due to below ground production which was not measured in our study. In the nearby Gulf of Carpentaria in Australia the gross carbon production (not including losses due to respiration) for seagrass meadows of the same species as ours were often lower than the net production values we recorded at Orman Reefs (Moriarty *et al.* 1990). Measurements of mixed species seagrass meadows similar in species composition to our site in Indonesia also had a relatively low net carbon production of 0.06 to 1.06 g C m⁻² day⁻¹ (Lindeboom & Sandee 1989). While production at Orman Reefs was high compared with other tropical locations, net carbon production in some dense temperate seagrass meadows can be much higher such as for *Zostera marina* which can range from 1.7 to 10.3 g C m⁻² day⁻¹ (Stevenson 1988).

Compared with other shallow aquatic environments seagrasses are generally considered to be one of the most highly productive habitats (Duarte and Cebrian 1996; Duarte and Chiscano 1999; Margalef 1986; Stevenson 1988) and our study supports this. The net primary productivity of seagrass meadows at Orman Reefs was higher than that determined for a mangrove forest in north Queensland (0.953 g C m⁻² day⁻¹) (Clough 1998) and higher than many freshwater and brackish autotrophic communities (Stevenson 1988). The net above ground productivity of seagrasses in our study also compared well with and often exceeded that of many terrestrial plant communities including tropical and temperate forests and grasslands (Duarte and Chiscano 1999; Gower *et al.* 2001).

The net primary production of the reef platform seagrasses at Orman Reefs is likely to be an important source of carbon for marine ecosystems in the greater Torres Strait region. Sources of marine autotrophic production are of critical importance in the area due to the general lack of terrestrial sources of carbon. The large area of seagrass at Orman Reefs (21,600 ha) represented a substantial proportion of the available shallow seagrass habitat of the central Torres Strait. Carbon stable isotope analysis in Torres Strait food webs has also demonstrated that seagrasses were a key source of carbon for animals in intertidal areas compared with other primary producers such as macroalgae, phytoplankton and epiphytic algae (Fry *et al.* 1983). The central Torres Strait area is also recognised as being of key importance for dugong and turtle populations (Marsh *et al.* 2004) with both species deriving the majority of their dietary requirements directly from seagrasses (André *et al.* 2005). A study of dugong and green turtle diets at Orman Reefs has shown that dugongs fed exclusively on seagrasses and that seagrasses constituted a large portion of green turtle diet (André *et al.* 2005).

The results of this study support the notion that the Orman Reef seagrass meadows may well be the “powerhouse of production” in the central Torres Strait. Not only are they important in supporting dugong and turtle populations but were also likely to provide habitat and nursery grounds for many other species including commercially important prawns and tropical rock lobster. This study however, demonstrated that these meadows were likely to vary considerably seasonally and there is evidence of considerable variation between years as well. This variability is likely to have consequences for the species and ecosystems depending on seagrasses for habitat and as a source of primary production.

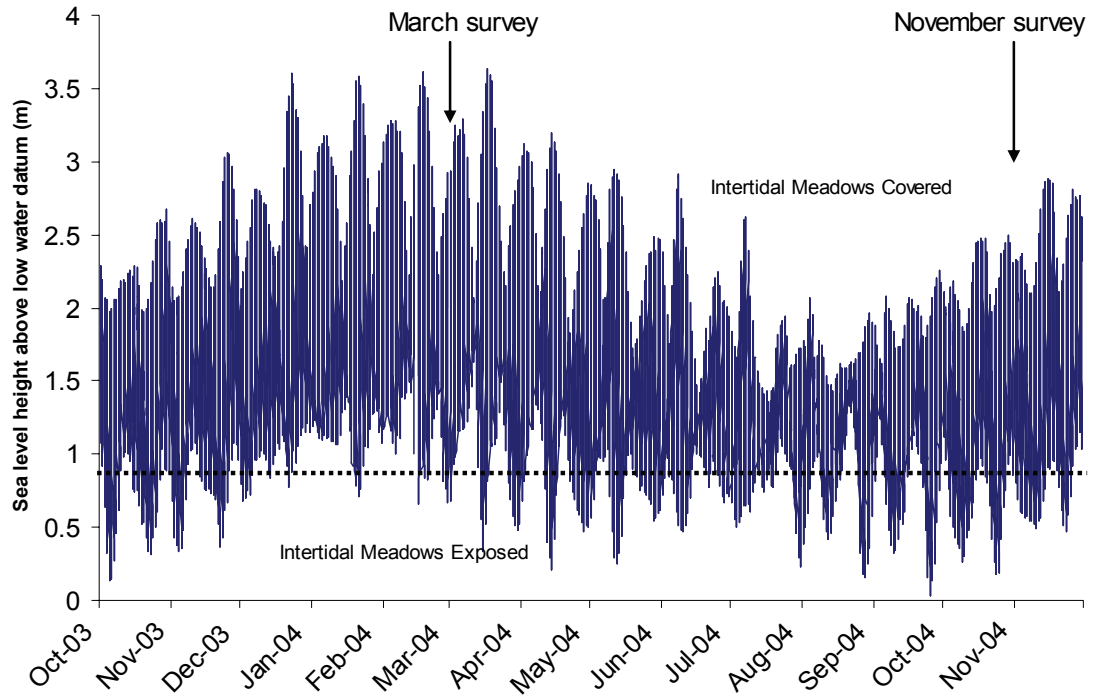


Figure 4. Sea level height during daylight hours and exposure of intertidal seagrass meadows for Orman Reefs from October 2003 to December 2004.

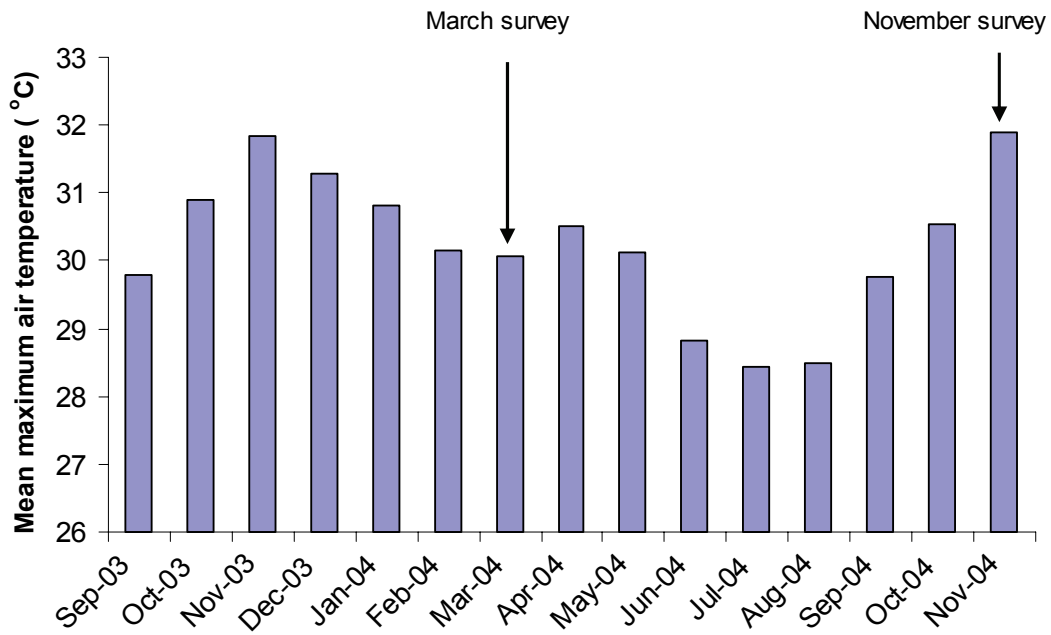


Figure 5. Mean monthly maximum air temperature and for Thursday Island (September 2003 to November 2004)

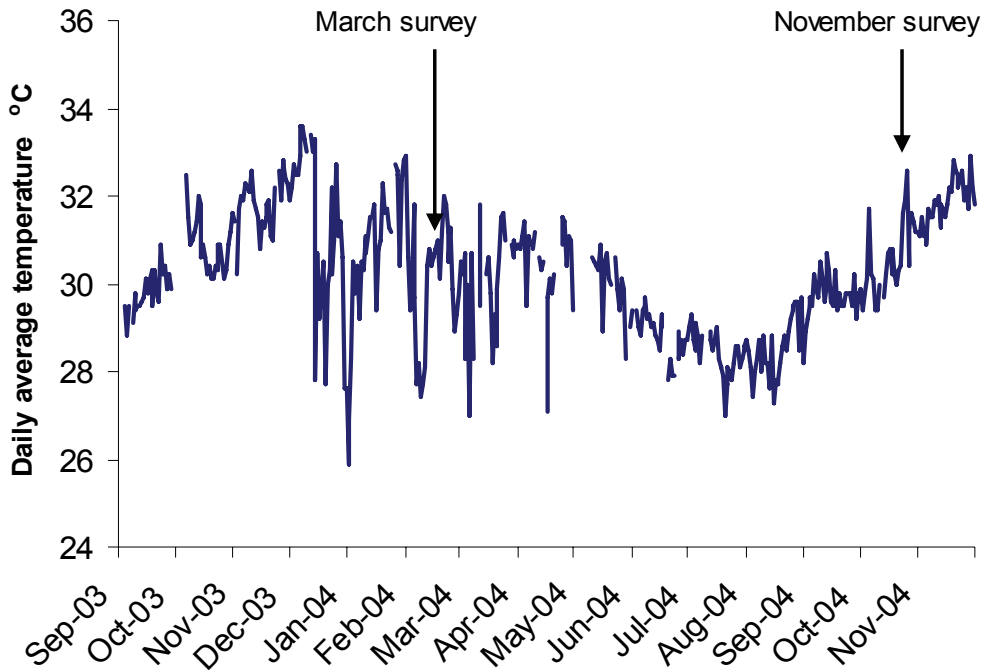


Figure 6. Daily average water surface temperature at Horn Island, Torres Strait (October 2003 to December 2004)

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