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Productivity, carbon assimilation and intra-annual change in tropical reef platform seagrass communities of the Torres Strait, north-eastern Australia

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Abstract

Detailed seagrass distribution, abundance, growth rates and community structure information was collected at Orman Reefs in March 2004 to estimate the above ground productivity and carbon assimilated by seagrass meadows. Seagrass meadows were re-examined in November 2004 for comparison at the seasonal extremes of seagrass abundance. Ten seagrass species were identified in the meadows on Orman Reefs. Extensive seagrass coverage was found in March (18,700 ha) and November (21,600 ha), with seagrass covering 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, distribution and species composition between the two surveys. Major changes between March and November included a substantial decline in biomass for intertidal meadows and an expansion in area of subtidal meadows. Changes were most likely a result of greater tidal exposure of intertidal meadows prior to November leading to desiccation and temperature related stress.

The Orman Reef seagrass meadows had a total above ground productivity of 259.8 t DW day^{-1} and estimated carbon assimilation of 89.4 t C day^{-1} in March. The majority of this production came from the intertidal meadows which accounted for 81% of the total production. Intra-annual changes in seagrass species composition, shoot density and size of meadows measured in this study were likely to have a strong influence on the total above ground production during the year. The net estimated above ground productivity of Orman Reefs meadows in March 2004 (1.19 g C m^{-2} day^{-1}) was high compared with other tropical seagrass areas that have been studied and also higher than many other marine, estuarine and terrestrial plant communities.

Key words

Seagrass; productivity; carbon; distribution; seasonality; Torres Strait

1. Introduction

Seagrass meadows are of great ecological importance and have been recognised as one of the most productive marine ecosystems (Green and Short 2003). 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 (Green and Short 2003). Coastal areas containing seagrass meadows have also been closely linked with high fisheries production, principally due to their value as a nursery habitat (eg Coles *et al*. 1993; Watson *et al*. 1993). In tropical areas, direct herbivory of seagrasses from 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 (Kaldy *et al.* 1999; Mateo *et al.* 2006).

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; Erftemeijer 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 (Rasheed 2004), herbivory (Klumpp *et al.* 1993), intraspecific competition (Rose and Dawes 1999), nutrients (Udy et al 1999) and flooding (Campbell and McKenzie 2004). The most common changes, however, occur as a result of seasonal factors. Seasonal changes in light, temperature and exposure are key drivers controlling seagrass biomass (Duarte *et al.* 2006), species composition (Bridges *et al.* 1982) and productivity (Duarte 1991) 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). In tropical locations other environmental factors such as changes to the duration of daytime exposure of intertidal meadows have also been found to be important in determining intra-annual seagrass change (Stapel *et al.* 1996). The influence of seasonal and environmental factors on seagrasses also varies between species. Marba *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 (Marsh *et al.* 2004) and similar meadows to the south are known to support commercially important fisheries (Watson *et al.* 1993). The sustainability of the Torres Strait traditional dugong fishery is a major imperative for Torres Strait peoples who greatly value dugongs for their nutritional, cultural, social, economic and ideological significance (Heinsohn *et al.* 2004). 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 Torres Strait underpins much of this fisheries and traditional hunting production.

The production and growth rates of many individual seagrass species have been measured (eg. Kenworthy *et al.* 1989; Erftemeijer *et al.* 1993; Bandeira 2002; Uku *et al.* 2005) but 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 Torres Strait may be strongly influenced by extremes in weather. Studies have shown substantial seagrass dieback (up to 60%) on two occasions in central Torres Strait (Long and Skewes, 1996; Marsh *et al*. 2004). The causes for these diebacks are unclear. Although suggested to be the result of flooding (Long and Skewes, 1996), recent investigations have shown that neither the movements of large sandbanks nor turbidity from rivers on the south coast of Papua New Guinea are likely to affect seagrass communities of Torres Strait on a regional scale (Daniell *et al*. 2006). Nevertheless, 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 describe in detail the seagrass distribution, abundance and community structure of a large tropical reef platform seagrass community in the central Torres Strait during the two seasonal extremes and use this information to provide an estimate of the above ground-productivity and carbon assimilated by the seagrass meadows.

2. Methods

2.1 Study area

Torres Strait is situated between Papua New Guinea and the most northern point of the Australian mainland. There are over 100 islands located in Torres Strait, 18 of which are inhabited. The region is tropical and dominated by two highly seasonal wind regimes: the north-west monsoon season from November to April and the south-east tradewind season from May to October (Williams 1994). The majority of the annual rainfall (average 1717 mm) falls during the north-west monsoon. Mean daily temperatures range from a minimum of 22.7ºC in July to a maximum of 32.1ºC in October. Water temperatures around Thursday Island to the south of Orman Reefs range between 24.4 and 27.7ºC (Pitcher *et al*. 1994), however water temperatures are likely to be higher in the central Torres Strait region.

The Orman Reefs are located in the central region of Torres Strait, approximately 10 kilometres northeast of Mabuiag Island (Fig. 1). The central region of 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 comprises six individual reefs, the main being Beka, Kai, Gariar and Anui which comprise 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.

2.2 Seagrass distribution abundance and community structure

Orman Reefs seagrasses were mapped and assessed in March (north-west monsoon season) and November (south-east trade wind season) 2004 to provide an indication of intra-annual variation in distribution and abundance. The extent of the surveys was the same in both March and November so that direct comparisons could be made and included all intertidal reef top areas and subtidal areas to approximately 1 nautical mile from the reef edge.

The large intertidal reef top areas were surveyed by helicopter at low tide when meadows were exposed. Boundaries of intertidal meadows were mapped using GPS (accurate to ± 5 m) during a low level flight (20-50m). Sites (radius 2 m) randomly located within intertidal meadows were assessed from the helicopter hovering within one metre above the substrate. Sampling intensity was stratified with a greater number of sites located in areas where habitat complexity was high. Subtidal meadows were ground-truthed by either free-diving (<7m) or surface controlled cable TV camera (>7m) at sites (radius 2 m) along transects and at isolated points. The position of each site was recorded using a GPS. Sites were located approximately every 500m on transects that extended from the intertidal edge of the reefs to the spatial limit of the survey. Transects were spaced from 1 to 3 km apart with a higher density of transects in areas of high habitat complexity. Additional sites between transects were sampled to check for seagrass habitat continuity. A van Veen grab (grab area 0.0625 m^2) was used at each subtidal site to confirm seagrass species and sediment characteristics.

To characterise meadows, observations on sediment type, depth below mean sea level (for subtidal sites), seagrass species composition and above ground biomass were recorded at each ground-truthed site. Sites were characterised by three random placements of a $0.25m^2$ quadrat. Seagrass above ground biomass was determined from each quadrat within a site, based on a modified “visual estimates of biomass” technique described by Mellors (1991).

Distribution maps of seagrass species, abundance and communities were generated using ArcGIS® (Environmental Systems Research Institute, Inc., Redlands, CA). The precision of determining seagrass meadow boundaries was expressed as an estimate of reliability (R) (see

McKenzie *et al*. 2001) and ranged from 50 m to 200 m. 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.

2.3 Above ground seagrass productivity

To determine the total above ground production, carbon produced and turnover time for Orman Reefs seagrass meadows, the information collected in the seagrass distribution abundance and community structure survey in March 2004 was combined with measurements of productivity for individual species and literature derived values of percent carbon for new growth (Fig. 1).

In March 2004 net above ground productivity data for each seagrass species found in the Orman Reefs meadows was collected from Anui Reef (Orman Reefs) and Thursday Island (90 km south of Orman Reefs) (see Fig. 2). Net above ground production of species was measured using a range of methods. For leaf replacing seagrass species the leaf growth rate was determined using the *in situ* leaf marking method (Short and Duarte 2001). A minimum of 30 shoots for each species were marked by punching a hole through all the leaves of an individual shoot just below the top of the basal meristem (sheath). Plants were harvested 3 to 8 days after marking and the biomass in grams of dry weight (g DW) of both new and old growth measured. For non-leaf replacing species, biomass (g DW) of new leaf material was measured using the rhizome tagging method described by Short and Duarte (2001). A minimum of 5 rhizomes were tagged for each species at the basal meristem and harvested 3 to 8 days after tagging. For the di-meristematic non-leaf replacing species, a leaf clipping method (Short and Duarte 2001) was used in addition to rhizome tagging. 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.

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 was multiplied by the biomass added for each shoot or basal meristem per day. Shoot and basal meristem densities for each species were determined by converting the above ground biomass for seagrass meadows (measured in the study) using values derived from other studies where both biomass and shoot density were recorded (Table 1). 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. 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.

Meadow above ground turnover times were calculated by dividing the meadow biomass determined from the surveys by the calculated meadow above ground productivity. To estimate the net above ground carbon production we used a conservative average value across all seagrass species of 34% of the total above ground dry weight. This was derived from other studies geographically and environmentally similar to the Orman Reefs (including Atkinson and Smith 1983; Koike *et al.* 1987; Erftemeijer 1994; Hemminga *et al*. 1995; Lobb JCU Unpublished data).

3. Results

3.1 Seagrass distribution abundance and community structure

Ten seagrass species were identified in the meadows on Orman Reefs (Table 2). Extensive seagrass coverage was found in March and November 2004 (Figs. 2 & 3), with seagrass covering 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, distribution and species composition between the two surveys.

In March 2004, 16 seagrass meadows were mapped within the survey area. The total area of seagrass was 18,683.9 ± 4,837 ha, of which 9,491.2 ± 2,257.7 ha was on the intertidal reef tops (Fig. 2; Table 3). Due to the outer extent of the survey being set at 1 nautical mile from the reef edge some subtidal seagrass meadows were likely to have continued beyond the survey limit. Individual meadow areas ranged from 10.3 ha to 6,905.5 ha (Fig. 2; Table 3). Intertidal meadows had moderate above ground biomass (mean = 31.8 ± 3.2 g DW m^{-2}) and were dominated by the structurally larger seagrass species *Thalassia hemprichii*, *Thalassodendron ciliatum* and *Enhalus acoroides* (Fig. 2; Table 3). Subtidal meadows were lower in biomass (mean = 13.1 ± 1.3 g DW m^{-2}) and were composed of varying community types, although generally dominated by the structurally smaller *Halophila* species (Fig. 2; Table 3).

In November 2004, 12 community types were identified and mapped in 17 individual meadows (Fig. 3; Table 4). Intertidal meadows were typically dominated by *T. hemprichii* and covered a similar area of the reef tops to March (9,491.2 ± 2,257.7 ha and 9,456.7 ± 2,097.3 ha respectively). These meadows had declined substantially in biomass with a 70% reduction (mean = 9.61 ± g DW m^{-2}). The only intertidal meadow in the November survey with a moderate biomass was a *T. ciliatum* dominated meadow on Gariar Reef (Meadow 6, mean = 46.24 g DW m^{-2}). The area of subtidal seagrass had increased in November to 12,144.8 ha

(32% increase) largely due to the expansion of meadows off the deeper eastern edges of the reefs (Fig. 3). Subtidal meadows were typically light in biomass (mean = 4.46 g DW m^{-2}) and dominated by *Halophila spinulosa* (Fig. 3; Table 4). Overall these meadows had a 66% reduction in biomass since March (Tables 3 & 4).

The total above ground biomass varied greatly between individual meadows according to the dominant species present. 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. 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 (Figs. 2 & 3; Tables 3 & 4).

The species composition of intertidal meadows was generally similar between March and November surveys although *Cymodocea serrulata* appeared to be less affected by the large declines in meadow biomass than other species (Tables 3 & 4). 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 the proportion of meadow biomass comprised by *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 (Figs. 2 & 3). Two of the smaller subtidal seagrass meadows (meadows 12 and 20) had disappeared between March and November and two new meadows had developed (meadows 14 and 18) (Figs. 2 and 3; Tables 3 & 4).

3.2 Above ground productivity of Orman Reefs seagrasses

3.2.1 Above ground production of seagrass species

Net seagrass above ground productivity varied markedly between species, according to shoot size (Table 5). The two structurally largest species, *E. acoroides* and *T. 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 *T. hemprichii*, *C. rotundata*, *Cymodocea serrulata* and *H. spinulosa* (Table 5). 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 x 10^{-4} g DW shoot^{-1} day^{-1}).

3.2.2 Above ground productivity of meadows

The Orman Reefs seagrass meadows had an estimated total net above ground productivity of 259.81 tonnes dry weight per day in March (Table 6). Intertidal meadows accounted for 81% of the total production. The large intertidal meadows on Beka, Kai and Gariar Reefs (meadows 3, 7, 9 and 19; Fig. 2) and the large subtidal meadow to the west of Orman Reefs (meadow 16) accounted for the majority of the above ground productivity (Fig. 2; Table 6).

Individual meadows dominated by *T. ciliatum* had the greatest productivity (from 4.9 to 9.9 g DW m^{-2} day^{-1}) but due to their relatively small size contributed only a minor component to the total above ground production at Orman Reefs (Tables 2 & 6). The 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}) but were much larger in size. These meadows were dominated by species with lower production per shoot such as *T. hemprichii* (Tables 3 & 6).

3.2.3 Meadow turnover

The time required for meadows to turn over their above ground biomass ranged from 9.6 to 26.8 days (Table 6). The majority of both intertidal and subtidal meadows could completely turn over their standing crop in approximately 10 days (Table 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 (Fig. 4). Meadows that were dominated by *E. acoroides* had the longest turnover time (22.4 to 25.7 days).

3.2.4 Above ground carbon production

It is estimated that the Orman Reefs seagrass meadows incorporated a total of 89.1 tonnes of carbon per day in March into their above ground biomass (Table 6). As with the overall above ground productivity the majority of carbon was added by the intertidal meadows (Table 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).

Mean carbon production varied considerably between meadows from <0.001 to 3.41 g C m^{-2} day^{-1} in March (Table 6). Meadows dominated by species that added the greatest biomass per day such as *T. ciliatum* and *E. 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 3 & 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 3 & 6).

4. Discussion

Compared with other shallow aquatic environments seagrasses are generally considered to be one of the most highly productive habitats (Margalef 1986; Stevenson 1988; Duarte and Cebrian 1996; Duarte and Chiscano 1999) and our study supports this. The net primary productivity of seagrass meadows at Orman Reefs in March 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).

Our study describes in detail the seagrass distribution, abundance and community structure of a large tropical reef platform seagrass community in 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 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 reef platform seagrasses described in northern Australia.

The diversity of seagrass species at Orman Reefs was high, with ten of the eleven known species to occur in Torres Strait observed (Bridges *et al.* 1982; Rasheed *et al.* 2003). 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 Halophila 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 intra-annual and 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).

At Orman Reefs it was likely that tidal exposure of intertidal meadows was a major influence in driving the observed biomass 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 (Fig. 5). This increased exposure also occurred at a time of year when daily maximum temperatures were reaching their annual peak (Bureau of Meteorology 2006). 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; Stapel *et al.* 1996). Similarly declines of intertidal *E. acoroides* meadows in Weipa approximately 250 km south of 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 lead 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. 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) and other *Halophila* species can be annual in Queensland only appearing late in the year (Kuo *et al.* 1993).

Above ground productivity and carbon assimilated by Orman Reefs seagrass meadows were likely to be strongly influenced by changes to species composition, shoot density and size of seagrass meadows. Intra-annual and seasonal change had a strong influence on all three of these factors and consequently were likely to have a strong effect on the total above ground production and carbon incorporated . Results of our study indicate that production was likely to be substantially lower in November than that measured in March. As intertidal meadows generally had higher shoot densities and covered a greater area they also contributed the majority of the production. Meadows dominated by the most productive species did not necessarily have the highest meadow productivity as they were either small in area (*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) 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 Bjork 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 (Vermaat *et al.* 1995; Longstaff *et al.* 1999; Udy *et al.* 1999; Knowles 2005).

Our study provides a “snapshot” of the above ground production and carbon assimilated by Orman Reefs seagrasses. It was likely however that the productivity and carbon assimilated would vary considerably from those estimated in March 2004. 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 (Moriarty *et al.* 1990; Marba *et al.* 1996; Uku and Bjork 2005; Duarte *et al.* 2006). *T. hemprichii*, for example, has been shown to have a large range in growth depending on the time of year (Uku and Bjork 2005). However growth rates of Orman Reefs seagrasses may not vary to the same extent, as the meadows are isolated from many of the terrestrial and anthropogenic influences such as nutrient runoff that were responsible for changes in seagrass productivity (Uku and Bjork 2005). In the absence of anthropogenic and terrestrial influences the key factors controlling seagrass growth rates relate to seasonal changes in light and temperature (Moriarty *et al.* 1990; Duarte *et al.* 2006;). Our measurements of seagrass growth were likely to be conservative as light and temperature conditions in 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 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 in other tropical locations (2.57 g DW m^{-2} day^{-1} compared with 1.58 g DW m^{-2} 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 g DW m^{-2} compared with 20.49 g DW m^{-2}) 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. Vermaat *et al.* 1995; Uku and Bjork 2005).

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 & Chiscano 1999) and this may be even higher when root production is included (up to 50 %, Duarte *et al.* 1998). A study in Papua New Guinea reported strong differences in the contribution to productivity made by below ground structures between many of the species that were also found at Orman Reefs (Brouns 1987) (17% for *T. hemprichii* 34% for *C. serrulata*, 50% for *C. rotundata* and 69% for *S. isoetifolium*).

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 around 10 days. Meadow turnover time was a reflection of the species composition with meadows dominated by *E. 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. accoroides* 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 g C m^{-2} day^{-1}) 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 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).

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 are a key source of carbon for animals in intertidal areas compared with other primary producers such as macro algae, phytoplankton and epiphytic algae (Fry *et al.* 1983).

The large intra-annual changes in the seagrass distribution and abundance at Orman Reefs are likely to have consequences for dugong and turtle feeding and foraging. Although seagrass biomass reduced substantially in the shallow intertidal areas in November there was a corresponding increase in *Halophila* dominated meadows in the deeper subtidal areas. This deeper *Halophila* would provide a potential food source for dugong of preferred seagrass species (Marsh *et al.* 1982; Sheppard *et al.* this edition) that may compensate for the declines in intertidal seagrass availability. Unlike dugong, green turtles in the Orman Reefs area are more flexible and opportunistic foragers, also feeding on macro-algae (Andre *et al.* 2005). In the event of any seagrass declines, green turtles therefore would have suitable alternative food resources.

It is possible that dugong and turtle grazing pressure may also have contributed to the observed intra-annual seagrass changes at Orman Reefs. Dugong grazing pressure can lead to significant species and biomass changes in seagrass meadows (Preen 1995). However, in our study the major changes were to intertidal meadows of species not generally preferred as a food source by dugong. Other factors such as tidal exposure remained the most likely drivers of the observed changes.

5. Conclusion

This study provides a detailed description of a substantial area of seagrass in the central Torres Strait. Measurements in March 2004 indicated that these meadows are highly productive compared to other tropical seagrass meadows and aquatic and terrestrial systems. The study also found that there is considerable intra-annual variation in distribution, abundance and species composition of seagrass meadows which is likely to have consequences for the species and ecosystems depending on them for habitat and as a source of primary production.

This study is one of the first to assess tropical seagrass productivity at a large regional scale and indicates that these meadows are likely to provide an important component of the primary productivity in the central Torres Strait region.

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Figure Captions

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

Figure 2. Seagrass distribution and community types for Orman Reefs in March 2004

Figure 3. Seagrass distribution and community types for Orman Reefs in November 2004

Figure 4. Above ground turnover time for Orman Reefs seagrass species in March 2004. 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.*

Figure 5. Total monthly hours of daytime exposure of intertidal seagrass meadows for Orman Reefs from October 2003 to December 2004.

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

Table 2. Seagrass species found in the Orman Reefs survey area, March and November 2004.

Family	Genus	Species	Source
CYMODOCEACEAE Taylor	*Cymodocea*	*rotundata*	Ehrenb. Et Hempr. Ex Aschers
	Cymodocea	*serrulata*	(R.Br.) Aschers. and Magnus
	Halodule	*uninervis*	(Forsk.) Aschers. in Boissier
	Syringodium	*isoetifolium*	(Aschers.) Dandy
	Thalassodendron	*ciliatum*	(Forsk.) den Hartog
HYDROCHARITACEAE Jussieu	*Enhalus*	*acoroides*	(L.F.) Royle
	Thalassia	*hemprichii*	(Ehrenb.) Aschers. in Petermann
	Halophila	*ovalis*	(R. Br.) Hook. F.
	Halophila	*spinulosa*	(R. Br.) Aschers. In Neumayer
	Halophila	*decipiens*	Ostenfeld

Table 3. Species composition, mean above ground biomass and area of Orman Reefs seagrass meadows in March 2004

	Meadow Number (Figure 2)	Species present (% composition of biomass)	No. of sites	Mean Biomass (g DW m^{-2})	Area ± R (ha)
Intertidal	1	*T. hemprichii* (96), *H. ovalis* (4)	3	16.36 ± 2.44	322.5 ± 110.6
	2	*T. hemprichii* (83), *E. acoroides* (11), *H. ovalis* (6)	8	10.39 ± 2.64	389.92 ± 106.83
	3	*T. hemprichii* (97), *E. acoroides* (2), *H. ovalis* (1), *C. serrulata* (<1)	28	26.09 ± 3.17	3621.12 ± 650.09
	4	*T. ciliatum* (89), *T. hemprichii* (11)	6	99.35 ± 9.49	95.75 ± 51.32
	5	*T. hemprichii* (89), *E. acoroides* (10), *H. ovalis* (1)	7	23.22 ± 4.42	130.3 ± 66.96
	6	*T. ciliatum* (79), *E. acoroides* (15), *T. hemprichii* (6)	3	97.60 ± 2.79	112.84 ± 53.12
	7	*T. hemprichii* (97), *E. acoroides* (3), *H. ovalis* (<1)	19	19.97 ± 1.83	1239.66 ± 389.85
	8	*E. acoroides* (68), *T. hemprichii* (32)	7	53.28 ± 5.95	480.43 ± 125.98
	9	*E. acoroides* (75), *T. hemprichii* (25)	9	45.26 ± 7.58	1190.94 ± 257.31
	19	*T. hemprichii* (54), *E. acoroides* (43), *H. ovalis* (3), *C. serrulata* (<1)	20	21.31 ± 5.31	1848.25 ± 297.50
	Sub-total		110	31.82 ± 3.22	9491.24 ± 2257.65
Subtidal	11	*C. serrulata* (83), *S. isoetifolium* (17)	3	0.01 ± 0.01	239.00 ± 125.77
	12	*H. spinulosa* (100)	2	0.03 ± 0.01	45.83 ± 30.43
	15	*T. ciliatum* (100)	4	52.63 ± 12.52	97.95 ± 91.61
	16	*T. hemprichii* (32), *H. spinulosa* (18), *C. serrulata* (16), *H. ovalis* (15), *S. isoetifolium* (10), *T. ciliatum* (6), *C. rotundata* (1), *H. uninervis* (1), *E. acoroides* (1)	73	7.15 ± 1.40	6905.46 ± 2027.35
	17	*H. spinulosa* (89), *H. ovalis* (11)	16	0.01 ± 0.01	1907.78 ± 445.59
	20	*T. ciliatum* (100)	1	48.96 ± 6.67	10.31 ± 6.72
	Sub-total		99	13.08 ± 1.31	9192.63 ± 2579.38
	TOTAL		209	20.49 ± 1.99	18,683.9 ± 4,837

Table 4. Species composition, mean above ground biomass and area of Orman Reefs seagrass meadows in November 2004

	Meadow Number (Figure 3	pecies present % composition of biomass)	No. of sites	Mean Biomass (g DW m^{-2})	Area ± R (ha)
Intertidal	1	*T. hemprichii* (65), *C. serrulata* (28), *H. ovalis* (7)	6	3.11 ± 0.89	322.6 ± 110.6
	2	*T. hemprichii* (71), *C. serrulata* (12), *H. spinulosa* (6), *C. rotundata* (5), *H. ovalis* (2), *T. ciliatum* (4)	13	7.50 ± 1.61	389.9 ± 106.8
	3	*T. hemprichii* (86), *C. serrulata* (9), *E. acoroides* (2), *C. rotundata* (2), *H. ovalis* (1)	31	7.49 ± 1.85	3232.9 ± 633.9
	4	*T. ciliatum* (86), *T. hemprichii* (6), *E. acoroides* (3), *S. isoetifolium* (3), *C. serrulata* (2)	4	33.82 ± 6.73	32.8 ± 30.7
	5	*E. acoroides* (43), *T. hemprichii* (34), *C. serrulata* (10), *T. ciliatum* (9), *H. ovalis* (2), *C. rotundata* (2)	14	5.74 ± 2.93	243.0 ± 71.0
	6	*T. ciliatum* (92), *E. acoroides* (3), *T. hemprichii* (3), *S. isoetifolium* (1), *H. ovalis* (1)	6	46.24 ± 4.28	136.8 ± 78.5
	7	*T. hemprichii* (70), *C. serrulata* (17), *C. rotundata* (6), *H. ovalis* (6)	23	3.47 ± 0.92	1197.5 ± 359.6
	8	*E. acoroides* (64), *T. hemprichii* (20), *C. serrulata* (17), *C. rotundata* (6), *H. ovalis* (1)	10	13.11 ± 5.90	474.1 ± 138.0
	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	1607.3 ± 243.9
	10	*E. acoroides* (56), *T. hemprichii* (23), *C. serrulata* (17), *C. rotundata* (3), *H. ovalis* (2)	5	10.60 ± 6.12	71.2 ± 31.0
	19	*T. hemprichii* (72), *C. serrulata* (12), *E. acoroides* (10), *H. ovalis* (5), *C. rotundata* (1), *H. uninervis* (<1)	57	6.09 ± 2.43	1748.6 ± 293.4
	Sub-total		186	9.61 ± 0.87	9456.7 ± 2097.3
Subtidal	11	*H. spinulosa* (88), *H. decipiens* (9), *C. serrulata* (1), *T. hemprichii* (1), *S. isoetifolium* (1), *H. ovalis* (<1)	17	2.08 ± 1.11	1208.9 ± 300.0
	14	*T. hemprichii* (100)	1	0.01	19. 8 ± 8.8
	15	*T. hemprichii* (92), *T. ciliatum* (8)	5	6.28 ± 2.57	150.1 ± 107.9
	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 ± 2156.8
	17	*H. spinulosa* (89), *H. decipiens* (11), *T. hemprichii* (<1)	22	2.86 ± 1.32	3003.0 ± 749.7
	18	*S. isoetifolium* (92), *H. ovalis* (5), *C. serrulata* (3)	3	7.80 ± 0.03	22.7 ± 19.0
	Sub-total		125	4.46 ± 0.72	12144.8 ± 3342.1
	Total		311	7.57 ± 1.63	21601.5 ± 5439.5

Table 5. Rate of new growth per shoot (g) used to determine above ground productivity and turnover time of seagrass meadows at Orman Reefs in March and November, 2004.

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

*value for *T. ciliatum* is for leaf growth only

Table 6. Above ground production, carbon production and meadow turnover time for Orman Reefs seagrass meadows in March 2004

	Meadow Number (Figure 1)	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)
Intertidal	1	5.485	1.701	1.886	0.585	9.62
	2	3.882	0.995	1.335	0.342	10.44
	3	95.086	2.626	32.705	0.903	9.94
	4	9.502	9.924	3.268	3.413	10.01
	5	2.824	2.168	0.971	0.746	10.71
	6	9.647	8.542	3.315	2.938	11.43
	7	24.658	1.989	8.481	0.684	10.04
	8	11.438	2.381	3.934	0.819	22.38
	9	20.961	1.760	7.210	0.605	25.72
	19	26.548	1.436	9.131	0.494	14.84
	Sub-total	210.024	3.352	72.239	1.153	
Subtidal	11	0.001	<0.001	<0.001	<0.001	26.81
	12	0.001	0.003	<0.001	<0.001	9.69
	15	5.136	5.244	1.767	1.804	10.04
	16	44.131	0.639	15.179	0.220	11.19
	17	0.014	0.001	0.005	<0.001	13.45
	20	0.503	4.878	0.173	1.678	10.04
	Sub-total	49.787	1.794	17.124	1.233	
	TOTAL	259.81	2.57	89.36	1.19	

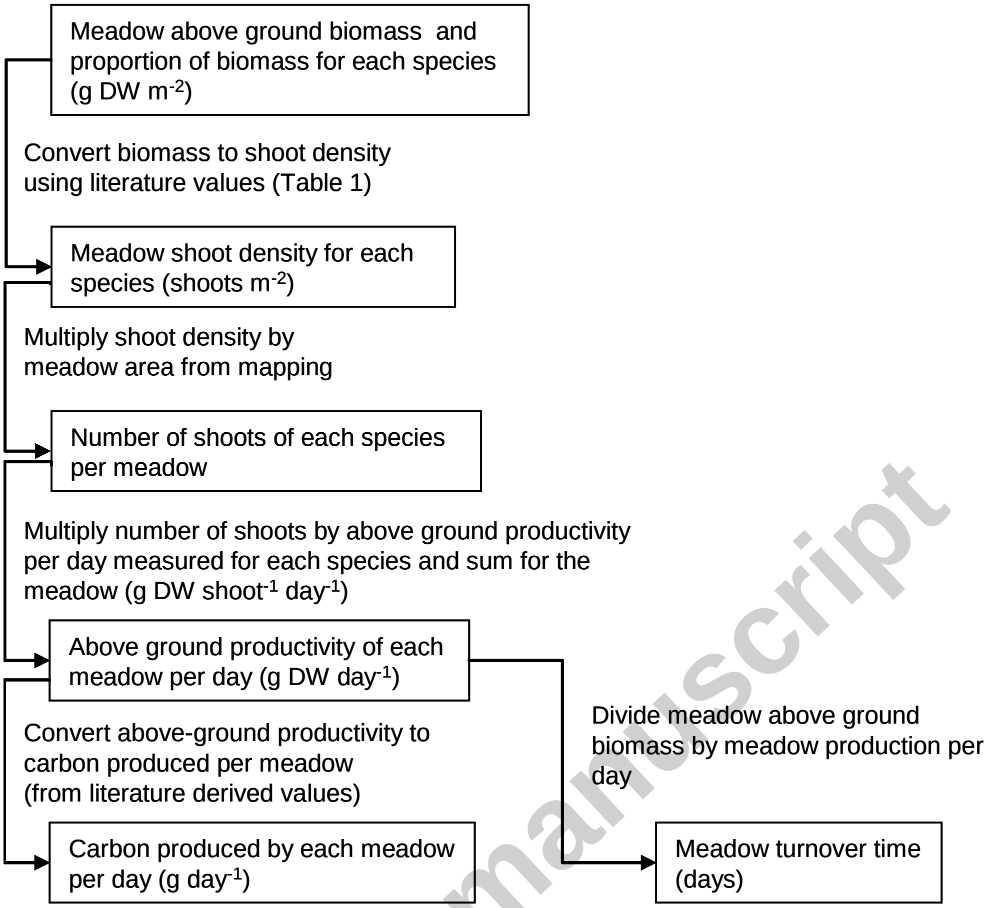

Figure 1. Flow chart detailing methodology for calculating above ground primary productivity, carbon assimilated and turnover time for seagrass meadows at Orman Reefs

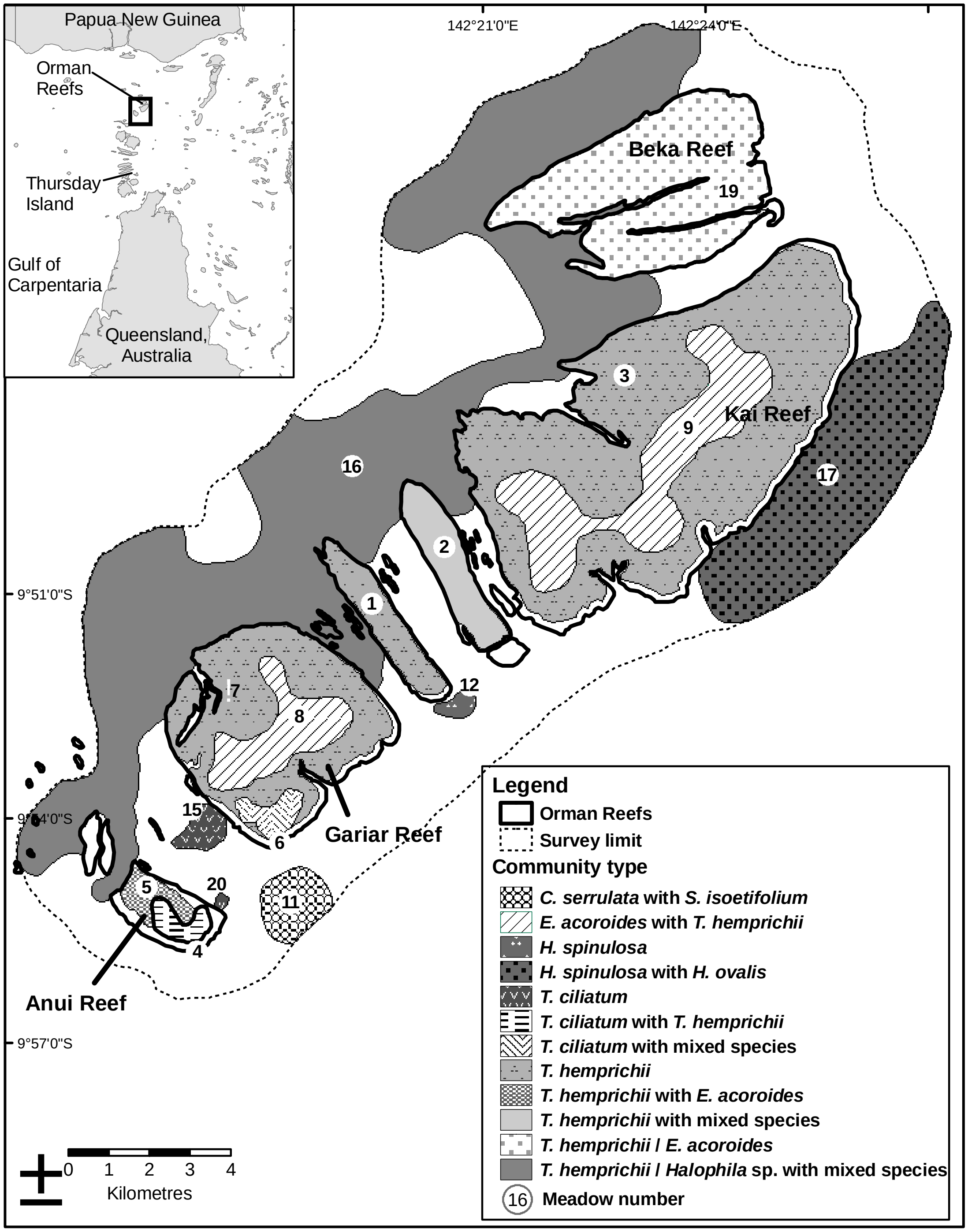

Figure 2. Seagrass distribution and community types for Orman Reefs in March 2004

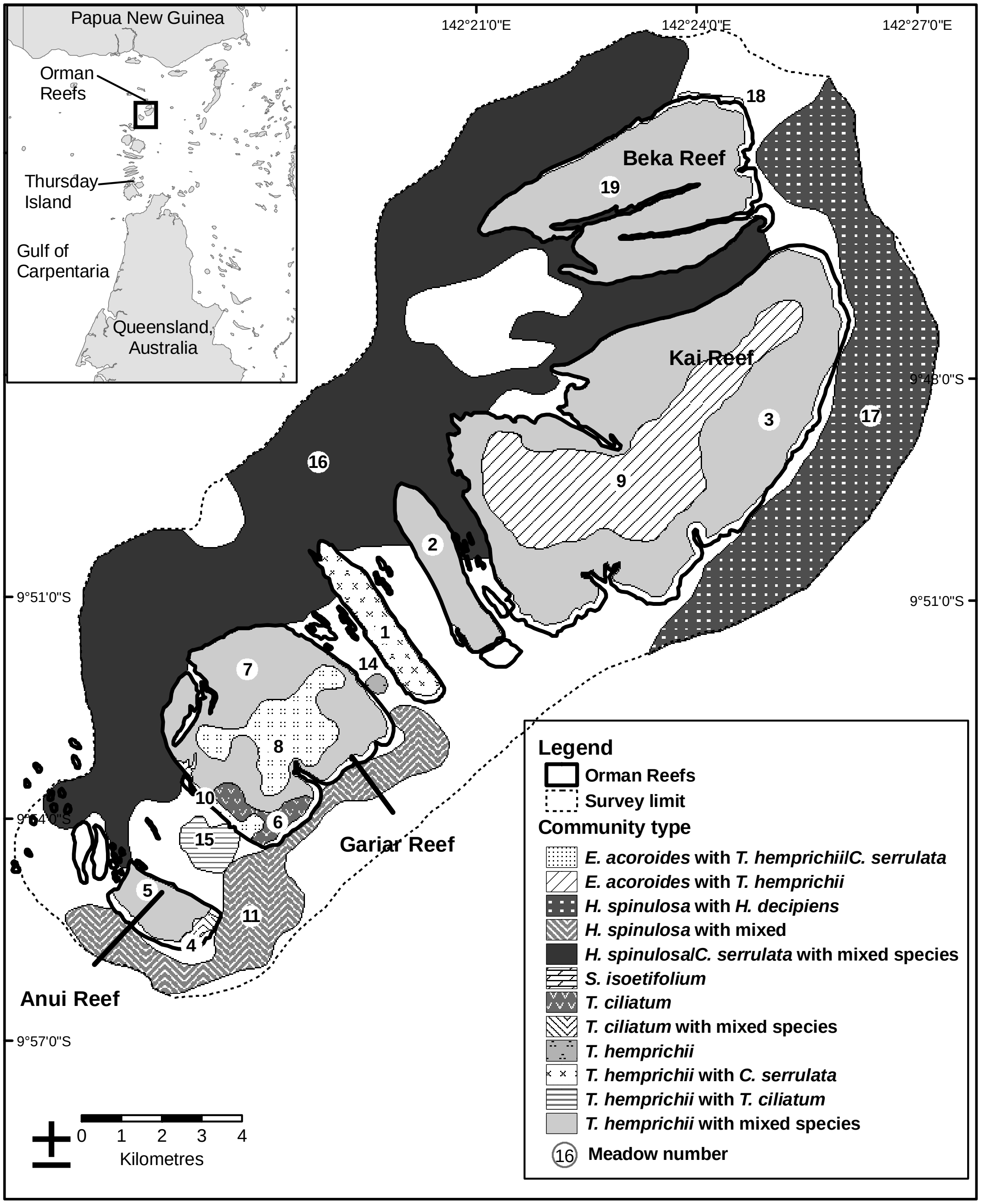

Figure 3. Seagrass distribution and community types for Orman Reefs in November 2004

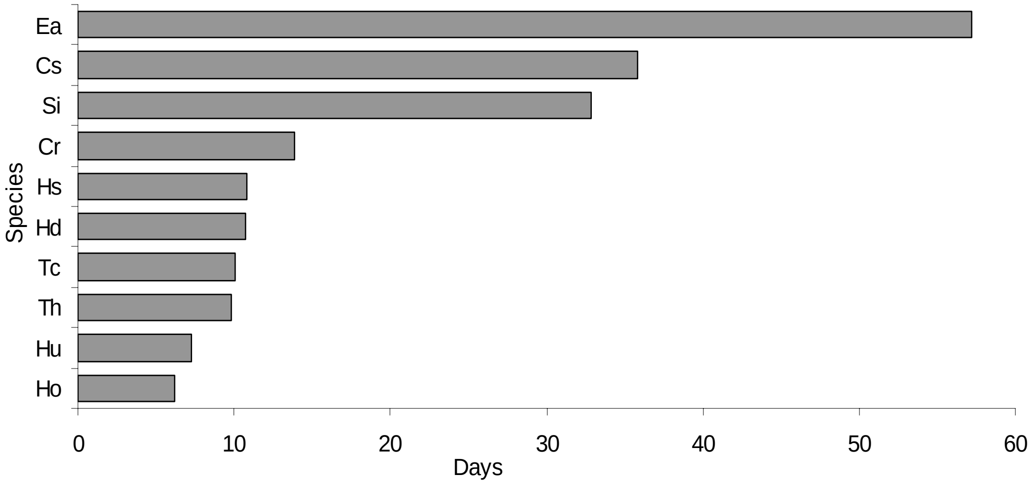

Figure 4. Above ground turnover time for Orman Reefs seagrass species in March 2004. Ea = *Enhalus acoroides*; Cs = *Cymodocea serrulata*; Si = *Syringodium isoetifolium*; Cr = *Cymodocea rotundata*; Hs = *Halophila spinulosa*; Hd = *Halophila decipiens*; Tc = *Thalassodendron ciliatum*; Th = *Thalassia hemprichii*; Hu = *Halodule uninervis*; Ho = *Halophila ovalis.*

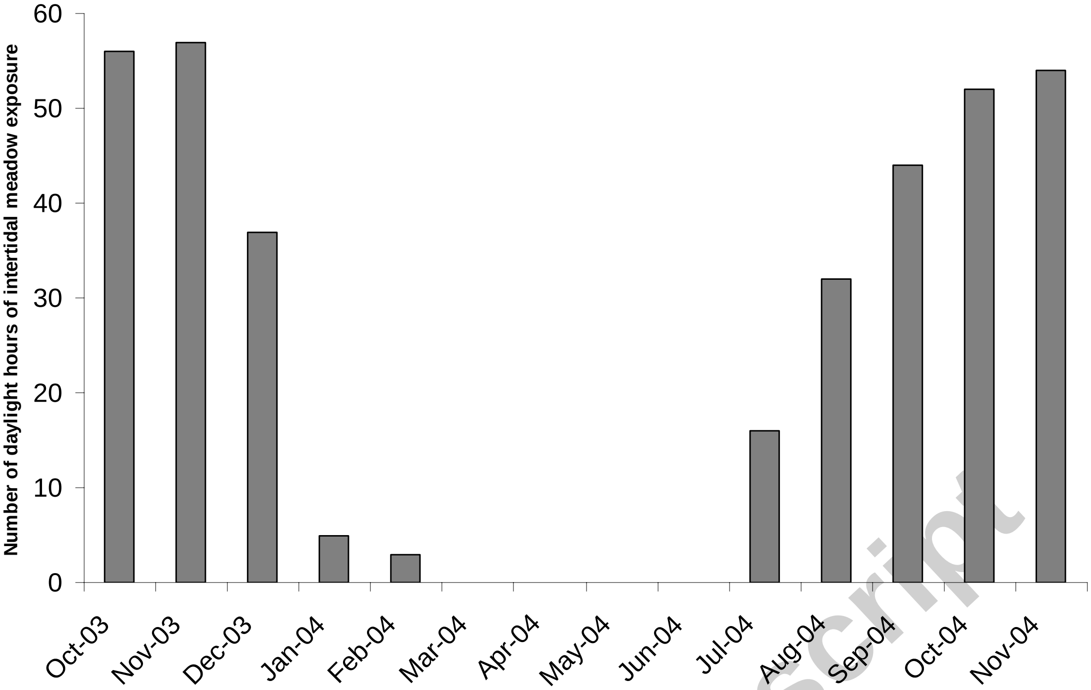

Figure 5. Total monthly hours of daytime exposure of intertidal seagrass meadows for Orman Reefs from October 2003 to December 2004.