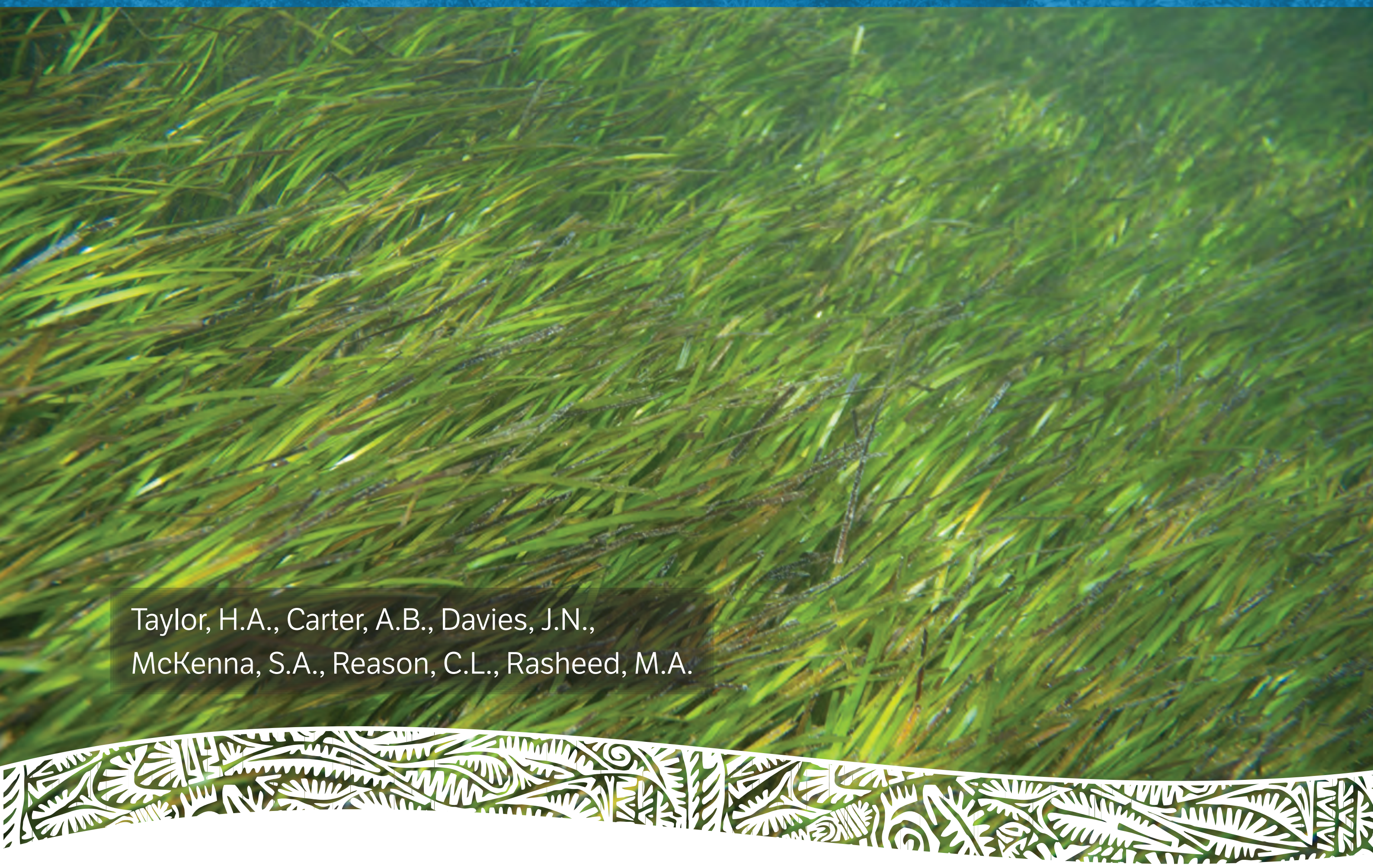
SEAGRASS PRODUCTIVITY, RESILIENCE TO CLIMATE CHANGE AND CAPACITY FOR RECOVERY IN THE TORRES STRAIT 2011-2013

Report No. 13/40

October 2013



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SEAGRASS PRODUCTIVITY, RESILIENCE TO CLIMATE CHANGE AND CAPACITY FOR RECOVERY IN THE TORRES STRAIT
2011-2013

A Report for Torres Strait Regional Authority
(TSRA)

Report No. 13/40

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EXECUTIVE SUMMARY

- The Tropical Water & Aquatic Ecosystem Research (TropWATER) Seagrass Ecology Group in collaboration with the Torres Strait Regional Authority Land and Sea Management Unit (TSRA LSMU) established a program to develop critical information for the management of dugong and turtle in the Torres Strait by understanding how their key food resource, seagrass, is affected by seasonal change, climate and their ability to recover from impacts. The project also provides key information on how seagrasses in the Torres Strait may be affected by climate change and how this may impact on turtle and dugong management.

- Several experimental sites were set up on intertidal and subtidal seagrass meadows examining seagrass recovery, productivity and potential environmental and climate drivers of change including light, exposure, temperature and salinity.
- Seagrasses at Mabuiag Island undergo distinct seasonal and inter-annual changes in biomass due to environmental conditions. Daytime tidal exposure and rainfall were identified as the environmental variables contributing most significantly to temporal variation in intertidal seagrass biomass at Mabuiag Island.
- The recovery experiments found that there were strong differences between meadow locations (subtidal and intertidal) and species in their capacity for recovery and the mechanisms employed to recolonise from disturbances. For intertidal mixed species meadows in this study, asexual colonisation was the most important mechanism for early recolonisation of cleared plots (gaps), whilst in the subtidal, recovery via a combination of sexual and asexual means was evident.
- Most seagrass species at Mabuiag Island would likely be able to recover from small scale disturbances over a period of months where adult plants remain by capitalising on their highly clonal nature. However, recovery from larger scale disturbances would depend more heavily on colonisation by sexual propagules and therefore take years to recover, if at all.
- Productivity levels of Mabuiag Island seagrasses compare with other globally important ecosystems. The net primary productivity of the intertidal meadow at Mabuiag Island at its peak in October (0.88 g C m^{-2} day^{-1}) was comparable to that of sub-tropical coastal seagrasses at Gladstone, Queensland (0.89 g C m^{-2} day^{-1}), and far above terrestrial grassland systems (0.50 g C m^{-2} day^{-1}). This provides evidence that intertidal seagrasses at Mabuiag Island make a major contribution to local productivity and in supporting dugong and turtle populations.
- Predicted changes to climate variables in Torres Strait and the Pacific region could have far reaching consequences for local seagrass community distribution and structure, which in turn may have profound implications for local dugong, turtle and commercial fisheries species. Management of seagrass resources in the Torres Strait should be focused on reducing any anthropogenic impacts to seagrass so as to ensure resilience levels of local seagrass populations remain high.

We recommend continuation of the research program at Mabuiag Island to establish a stronger predictive set of relationships between key climate impacts to Torres Strait seagrasses. These relationships require data to be collected over several seasons and years to be fully developed. Results will provide much-needed information on how natural climate variability and future scenarios of climate change may impact seagrass meadows, and therefore dugong and turtle feeding opportunities. Information that is collected has the potential to be incorporated into models to predict the consequences of climate change scenarios on Torres Strait seagrass, and to develop appropriate dugong and turtle management strategies that respond to changes in seagrass distribution and communities.

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1 INTRODUCTION

1.1 Background

The Torres Strait region covers an area of more than 35,000 km^2 and is located on one of the world's most extensive continental shelves. It comprises 247 islands, eighteen of which are permanently inhabited. Local island communities in the Torres Strait are deeply connected to their sea country through their culture, economy, spirituality and social way of life. The health of their marine resources has been, and continues to be, vital to Torres Strait Islanders from a subsistence, commercial and cultural point of view. Seagrass ecosystems are of particular importance to Torres Strait Islanders as they support fisheries, dugong and turtle populations which are of key importance, as well as driving much of the marine primary productivity in the region.

The importance of seagrasses as structural components of coastal ecosystems is well recognised. Seagrass and algae beds have been rated the third most valuable ecosystem globally (on a per hectare basis) for ecosystem services, preceded only by estuaries and swamps/flood plains (Costanza et al. 1997). The Torres Strait is estimated to contain between 13,425 km^2 (Coles et al. 2003) and 17,500 km^2 (Poiner and Peterkin 1996) of seagrass habitat, providing critical habitat for commercial and traditional fishery species as well as important food resources for endangered dugong and green turtle populations (Marsh and Kwan 2008; Sheppard et al. 2008; Coles et al. 2003). The largest population of dugongs in the world is in Torres Strait (Marsh and Lawler 2002; Marsh et al. 1997), where the long-standing importance of dugongs for subsistence by Torres Strait Islanders has been traced in archaeological deposits dating back at least 7000 years (Wright 2011; Vanderwal 1973). For the indigenous people of Torres Strait, the dugong is the most significant and highest ranked traditional subsistence marine food source (Kwan 2002; Johannes and MacFarlane 1991; Raven 1990; Nietschmann 1984).

The dynamics of Torres Strait seagrasses may be strongly influenced by natural and anthropogenic pressures. At the Orman Reefs, Torres Strait, the biomass and growth of seagrasses can vary by up to a factor of 3.5 during one year (Rasheed et al. 2008) while in South East Asia, they can vary by a factor of four (Lanyon and Marsh 1995; Erftemeijer and Herman 1994; Brouns 1985). 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 1987), seasonality of environmental factors (McKenzie 1994; Mellors et al. 1993) and flooding (Campbell and McKenzie 2004). Studies have shown substantial seagrass dieback (up to 60%) on two occasions in central Torres Strait (Marsh et al. 2004; Long and Skewes 1996). have been linked to declines in the dugong population (Marsh et al. 2004). Flooding initially was suggested as a cause for these diebacks (Long and Skewes 1996), but recent investigations have demonstrated 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 at a regional scale (Daniell et al. 2006).

A lack of experimental studies in the Torres Strait that quantify the impacts to seagrass from physical disturbances such as shipping accidents, or environmental change associated with climate and predicted climate change, limits our ability to predict the consequences of disturbance on seagrass habitats and their associated ecosystems and fisheries. This is despite the acknowledgement that the potential for impacts from shipping activities is very high (Queensland Transport and GBRMPA 2000) and Torres Strait ecosystems are likely to be particularly vulnerable to the effects of climate change (Suppiah et al. 2007). Seagrasses around the Orman Reefs in particular were identified as one of the most important areas of seagrass habitat in the Torres Strait and Queensland for dugong (Taylor and Rasheed 2010; Chartrand et al. 2009; Rasheed et al. 2008). Rasheed et al. (2008) determined that the above-ground productivity of the Orman Reef seagrass meadows was high compared with other tropical seagrass communities and likely to be a key contributor to fisheries production, supporting dugong and turtle populations and carbon cycling in the central Torres Strait. Understanding the dynamics of these seagrass communities and how they may be impacted by climate change, and the ability of seagrasses to recover from impacts, are critical knowledge when developing effective management strategies for dugong and turtle that depend on seagrass for food.

1.2 Sampling approach

The Tropical Water & Aquatic Ecosystem Research (TropWATER) Seagrass Ecology Group in collaboration with the Torres Strait Regional Authority (TSRA) Land and Sea Management Unit (LSMU) launched a program to develop critical information for the management of dugong and turtle in the Torres Strait by understanding how their key food resource, seagrass, is affected by seasonal change, climate, and their ability to recover from impacts. The project also provides key information on how seagrasses in the Torres Strait may be affected by climate change and how this may impact on turtle and dugong management.

The specific objectives of the present study were to:

1. Determine the importance of light, temperature and water quality in changes in seagrass meadow biomass at intertidal and subtidal meadows;
2. Determine the capacity for recovery following disturbance of seagrass meadows, including the roles of sexual and asexual reproduction; and
3. Measure above-ground and below-ground seagrass productivity and examine how productivity changes over time, particularly between seasons.

This report details data collected from April 2011 to June 2013.

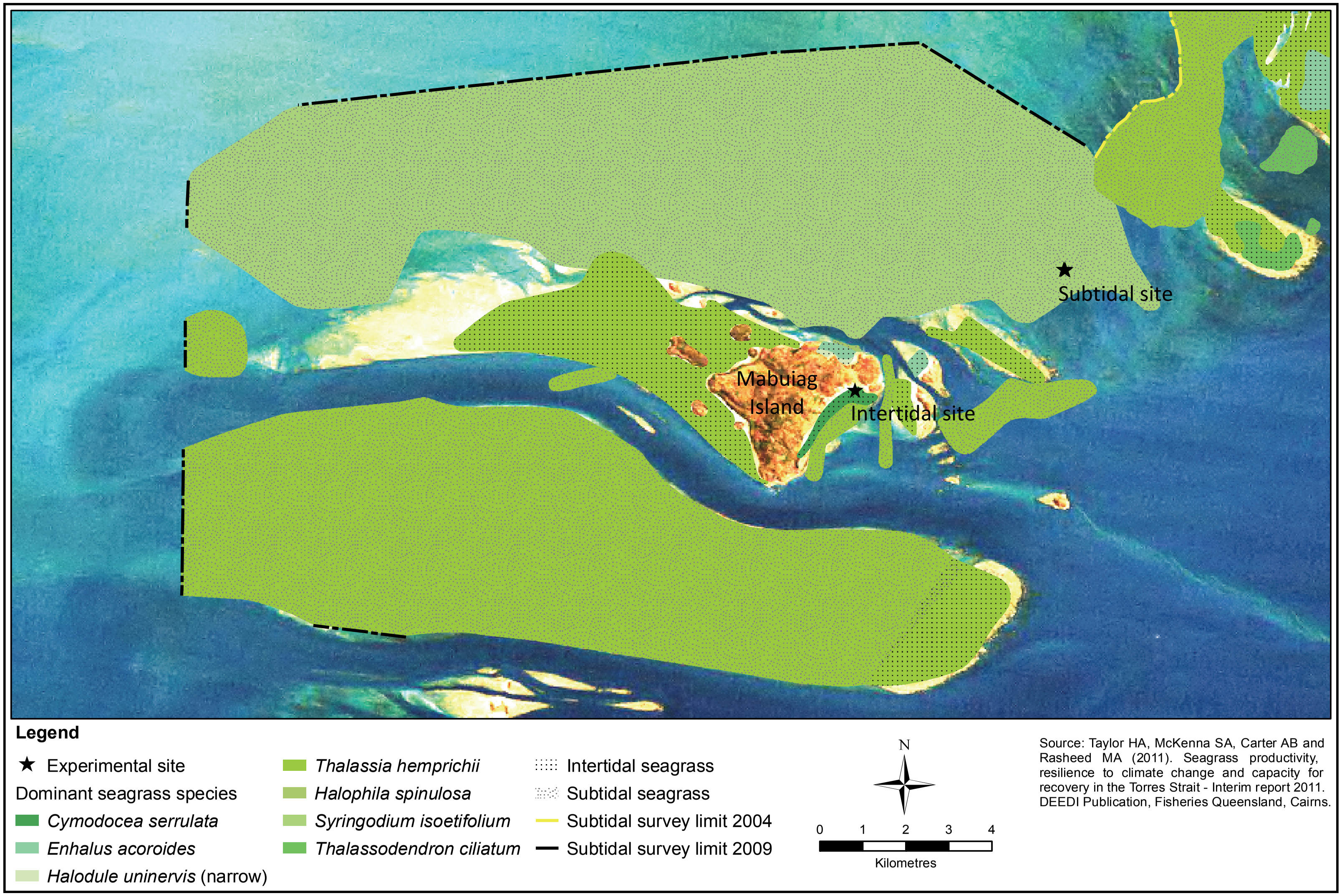
1.3 Study location

Mabuiag Island is in the Western region of the Torres Strait, approximately 100 kilometres north of Thursday Island. It once formed part of the now submerged land bridge that joined Australia with Papua New Guinea. A baseline assessment of intertidal and subtidal regions surrounding Mabuiag Island in 2009 and 2010 revealed extensive coverage of diverse seagrass meadows (Figure 1). These seagrasses, along with those at the nearby Orman Reefs, were identified as one of the most important areas in Queensland of seagrass habitat for dugong (Chartrand et al. 2009; Rasheed et al. 2008). Additionally, the above-ground productivity of Orman Reef seagrass meadows was high compared with other tropical seagrass communities, indicating that the habitat is likely to be important to fisheries, dugong and turtle, and carbon cycling in the central Torres Strait (Rasheed et al. 2008).

Manipulative seagrass experiments were set up in March/April 2011 in one subtidal and one intertidal location (Figure 1) where the seagrass assemblage reflected 'typical' community types in the region. A second round of recovery experiments only was established in late August 2011 (intertidal) and early November 2011 (subtidal) to determine if recovery of seagrasses were affected by seasonal change.

The experimental design for the recovery experiments (Section 3) involved three experimental blocks that were subject to a randomised block design of 12 (0.25 m^2) treatment plots of seagrass. Within each block, the 12 plots were subject to three replicates of four different treatments. The seagrass data used to examine climate-related change (Section 2) comes from the control, unbordered replicates within the experimental blocks. Finally, productivity measurements (seed cores, rhizome tagging and leaf marking; Section 4) were conducted on seagrass near to the recovery experimental blocks.

Figure 1. Location of subtidal and intertidal seagrass around Mabuiag Island (2009-2010) and Orman Reefs (2004), and location of seagrass manipulative experiments (2011-2013).



2 LOCAL CLIMATE, BENTHIC PAR AND SEASONAL SEAGRASS TRENDS

2.1 Introduction

Light, temperature, exposure and nutrients affect biochemical processes of organisms, and are considered as major factors controlling seagrass growth (Duarte et al. 2006; Mellors 2003). Many of these factors vary with lunar cycles, among seasons, and annually. Tropical seagrass meadow biomass typically varies among seasons (Rasheed 2004; Rasheed 1999; McKenzie 1994) and among years (eg. Taylor and Rasheed 2011; Chartrand et al. 2010). Tropical Queensland seagrasses typically peak in distribution and abundance during late spring to early summer, and decline during winter (Rasheed 2004; Rasheed 1999; McKenzie 1994; Mellors et al. 1993). Recent studies at Hay Point and elsewhere in Queensland have demonstrated there can be considerable variation in the timing and extent of seasonality in different seagrass meadow types (Chartrand et al. 2008). Information on the extent of natural seasonal change in seagrass is essential when predicting the potential impacts of natural disturbances (e.g. cyclones, floods) and climate change on seagrass meadows.

This study examines seasonal and annual changes in seagrass biomass around Mabuiag Island, Torres Strait. Recent studies have identified the nearby Orman Reefs as one of the most important areas of seagrass habitat in the Torres Strait and Queensland for dugong (Rasheed et al. 2008). Baseline surveys and a community ranger monitoring program have also been conducted around neighbouring Badu and Moa Islands and the Dugong Sanctuary (Taylor and Rasheed 2012; Taylor 2011; Taylor and Rasheed 2010). Extensive seagrass coverage was also identified during baseline surveys around Mabuiag Island in 2009 and 2010 (Taylor and Rasheed 2010; Chartrand et al. 2009). Little information is known regarding seasonal and annual changes in important seagrass habitat around Mabuiag Island, however, and information on the possible environmental drivers of seagrass change in Torres Strait is lacking.

The objectives of the seasonal seagrass monitoring study were to:

1. Conduct quarterly monitoring of seagrass biomass at intertidal sites, and opportunistic monitoring of seagrass biomass at subtidal sites, to examine seasonal and annual variation in seagrass biomass;
2. Determine the effect of light, temperature, exposure, salinity and rainfall on seagrass meadow biomass in intertidal meadows.

2.2 Methods

Sampling methods followed those used in the established seagrass monitoring programs for baseline assessment at Mabuiag Island (Taylor and Rasheed 2010; Chartrand et al. 2009) and long-term seagrass monitoring for other Queensland Ports such as Thursday Island, Cairns, Mackay, Weipa and Karumba (see Campbell et al. 2003; Rasheed et al. 2003; Roelofs et al. 2003; Rasheed et al. 2001a; Rasheed et al. 2001b).

2.2.1 Seagrass biomass

Seagrass biomass was estimated from nine permanent $0.25m^2$ quadrats in the intertidal and subtidal meadows. The intertidal meadow was sampled approximately monthly from March 2011 – September 2012, then approximately quarterly from September 2012 – May 2013. The subtidal meadow was sampled opportunistically when the weather and tides allowed from March 2011 – December 2012. Seagrass species were recorded and above-ground biomass was estimated in intertidal and subtidal meadows using a “visual estimates of biomass” technique described by Mellors (1991). This technique involves an observer ranking seagrass biomass in the field in each quadrat while referring to a series of quadrat photographs of similar seagrass habitats for which the above-ground biomass has been measured. Two separate biomass ranking ranges were used: low biomass and high biomass. The relative proportion of the above-ground biomass of each seagrass species within each quadrat was 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 representative of the range of seagrass biomass in the survey. After ranking, seagrass in these quadrats was harvested and the actual biomass determined in the laboratory. A separate linear 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.

2.2.2 Environmental monitoring

Environmental data (water temperature, light, salinity, rainfall, tidal exposure (intertidal meadows only), global solar exposure) were collected to model the impacts of climate on seagrass biomass in intertidal meadows. Three different in-situ loggers were used:

(i) Autonomous iBTag submersible temperature loggers recorded water temperature (°C) within the seagrass canopy every 15 minutes intertidally and 30 minutes subtidally (Plate 1A);

(ii) Submersible Odyssey™ photosynthetic irradiance autonomous loggers recorded light (measured as photosynthetically active radiation, PAR) every 15 minutes (Plate 1A); and

(iii) Submersible MX5 Sondes measured water temperature and salinity every 45 minutes (Plate 1B).

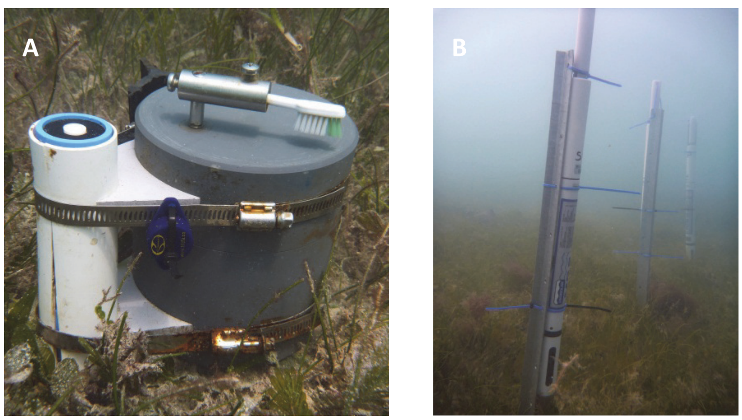


Plate 1. A) Autonomous iBTag submersible temperature logger (navy blue) attached to a "wiper unit" that cleans the surface of the Odyssey PAR logger (light blue) to prevent fouling; and B) three submerged MX5 Sonde units.

Total daily global solar exposure (GSE, megajoules per square metre; MJ m^{-2} day^{-1}) and total daily rainfall (mm) were obtained for the nearest weather station (Horn Island, station # 027058) from the Australian Bureau of Meteorology website (http://www.bom.gov.au/climate/data/). Tidal exposure for the intertidal meadow was calculated by summing the total daylight hours that the tidal height was $\leq$ 0.8m.Tidal data was provided by Maritime Safety Queensland (© The State of Queensland (Department of Transport and Main Roads) 2013, Tidal Data).

2.2.3 Statistical analyses

A Linear Mixed Effects Model (LME) was used to analyse the effects of season and year on above-ground biomass in the intertidal and subtidal meadows. For subtidal meadows we were unable to test for an interaction between season and year due to the limited number of sampling periods. Using LME models allowed for the seperation of explanatory variables into random (unplanned) and fixed (planned) effects. The repeated measurements of biomass taken at the quadrat level were not independent because the quadrats were fixed and because of temporal correlation. Fixed effects were the explanatory variables season and year and the random effect was quadrat. Autocorrelation of errors (repeated measures through time) was tested with an auto-regressive model of order one (AR(1) correlation). For subtidal measows we also compared models that did and did not account for heterogenous variances. Biomass data was square-root transformed prior to analysis for intertidal meadows and untransformed data was used for subtidal meadows. Diagnistic plots were used to check model assumptions (Pinheiro and Bates 2000). An ANOVA was then used to assess the significance of terms in the fixed effects part of the models (Pinheiro and Bates 2000) and to select the best fit model using Akaike Information Criterion (AIC) with the lowest AIC (Burnham and Anderson 2002). The LMEs were performed seperately for intertidal and subtidal meadows and conducted with the nlme package in R (intertidal meadows) (Pinheiro et al. 2007) and S-Plus (subtidal meadows).

For each of the twenty intertidal sampling periods (not including time zero) total GSE, total rainfall, total daytime tidal exposure, mean daily salinity, mean total daily PAR, mean daily water temperature, and maximum daily water temperature were determined for the 14, 30 and 90 days prior to the day seagrass biomass estimates were taken. These times periods were chosen to examine short-term (2 weeks – 1 month) and longer-term (3 months) effects of climate on seagrass.

Exploratory data analysis was conducted using scatter matrices for each environmental variable at each time period (14, 30, and 90 days) to identify correlations between biomass and environmental variables in intertidal meadows, and the most appropriate environmental variables to include in a Linear Model (LM). The environmental variables included in the LM were mean temperature (90d; Pearson's correlation coefficient = 0.58, $p < 0.05$), rainfall (30d; Pearson's correlation coefficient = 0.66, $p < 0.01$), maximum temperature (14d; Pearson's correlation coefficient = 0.54, $p < 0.05$) and exposure (30d; Pearson's correlation coefficient = 0.55, $p < 0.05$). Explanatory variables were tested for collinearity prior to fitting the models using variance inflation factors (VIF) (Zuur et al. 2009) in the car package (Fox and Weisberg 2009). When mean temperature was removed and the VIFs recalculated all VIFs were <3, indicating the set of explanatory variables did not contain collinearity (Zuur et al. 2009). There was no relationship between GSE and biomass, salinity and biomass, or PAR and biomass, so these variables were not included in the model.

To determine the optimal model we started with a global model where the fixed component considered all explanatory variables and up to 3-way interactions. Predictors were standardized to a mean of 0 and standard deviation of 0.5 using the "standardize" function in the R package 'arm' (Gelman et al. 2013). Sub-model sets of the global model were then generated and ranked according to the values of their Akaike's Information Criterion corrected for small sample size (AICc) using the dredge function in the MuMIn package in R (Barton 2013). Model averaging was performed to obtain average parameter estimates using functions in MuMIn on all models within two AICc of the best model (Burnham and Anderson 2002). Multi-model averaging was not possible for the subtidal meadow due to a lack of sampling events, but scatter matrices were created to identify potential environmental variables that may be influencing subtidal meadow biomass, subject to further sampling events. All analyses were conducted in R v.2.10.1. (R Development Core Team 2009).

2.3 Results

2.3.1 Seagrass biomass

Eight species of seagrass were recorded in the intertidal site. In decreasing order of abundance (biomass) they were: *Cymodocea serrulata, Cymodocea rotundata, Thalassia hemprichii, Halodule uninervis* (wide leaf morphology), *Syringodium isoetifolium, Halodule uninervis* (narrow leaf morphology), *Enhalus acoroides, Halophila ovalis,* and *Halophila spinulosa*. Subtidal seagrasses consisted of six seagrass species: *Syringodium* *isoetifolium, Halophila spinulosa, Cymodocea serrulata, Halophila ovalis, Halodule uninervis* (wide leaf morphology), and *Halophila decipiens*.

In the intertidal meadow season and year had a significant interaction affecting meadow biomass ($F_{3,155}$ = 6.8150, P < 0.001, Table 1). Biomass in 2011 was more variable than in 2012. In 2011 the lowest the biomass was recorded in autumn (32.2 $\pm$ 4.1 g DW m^{-2}) and the greatest biomass was recorded in the summer of 2011/2012 (65.9 $\pm$ 5.6 g DW m^{-2}) (Figures 2a, 3). In contrast, in 2012 biomass peaked in winter (47.8 $\pm$ 2.6 g DW m^{-2}) and reached a low in spring (43.6 + 1.7 g DW m^{-2}), although the range in meadow biomass was not as large as in 2011. Intertidal seagrass also varied among years. Autumn biomass values increased from 32.2 $\pm$ 4.1 g DW m^{-2} in 2011 to 59.6 $\pm$ 5.6 g DW m^{-2} in 2013 (Figure 2a; Plate 2).

For the subtidal meadow the best model took into account heterogeneous variances in seagrass biomass between sampling times but not autocorrelation. Season but not year had a significant effect on seagrass biomass ($F_{3,41}$ = 54.4355, P < 0.0001, Table 1). Biomass decreased between autumn and winter in 2011 and then increased during spring and summer. Peak biomass was recorded during summer in December 2011 (102.6 $\pm$ 5.5 g DW m^{-2}), but biomass was at its lowest level during a similar time of year in 2012 (December; 26.0 $\pm$ 6.6 g DW m^{-2}). Biomass was approximately 50 g DW m^{-2} during the autumn sampling periods in 2011 and 2012 (Figure 2b).

Table 1. Results from an ANOVA conducted to assess the significance of the fixed effects on the best Linear Mixed Effects Model for the biomass of intertidal (square-root transformed) and subtidal (untransformed data) seagrass biomass.

Meadow	Fixed effect	NumDF	DenDF	*F*-value	*P*-value
Intertidal	(Intercept)	1	155	1326.79	<.0001
	Year	1	155	7.19	0.0081
	Season	3	155	10.20	<.0001
	Year:Season	3	155	7.08	0.0002
Subtidal	(Intercept)	1	41	207.03	<.0001
	Year	1	41	1.18	0.2837
	Season	1	41	54.44	<.0001

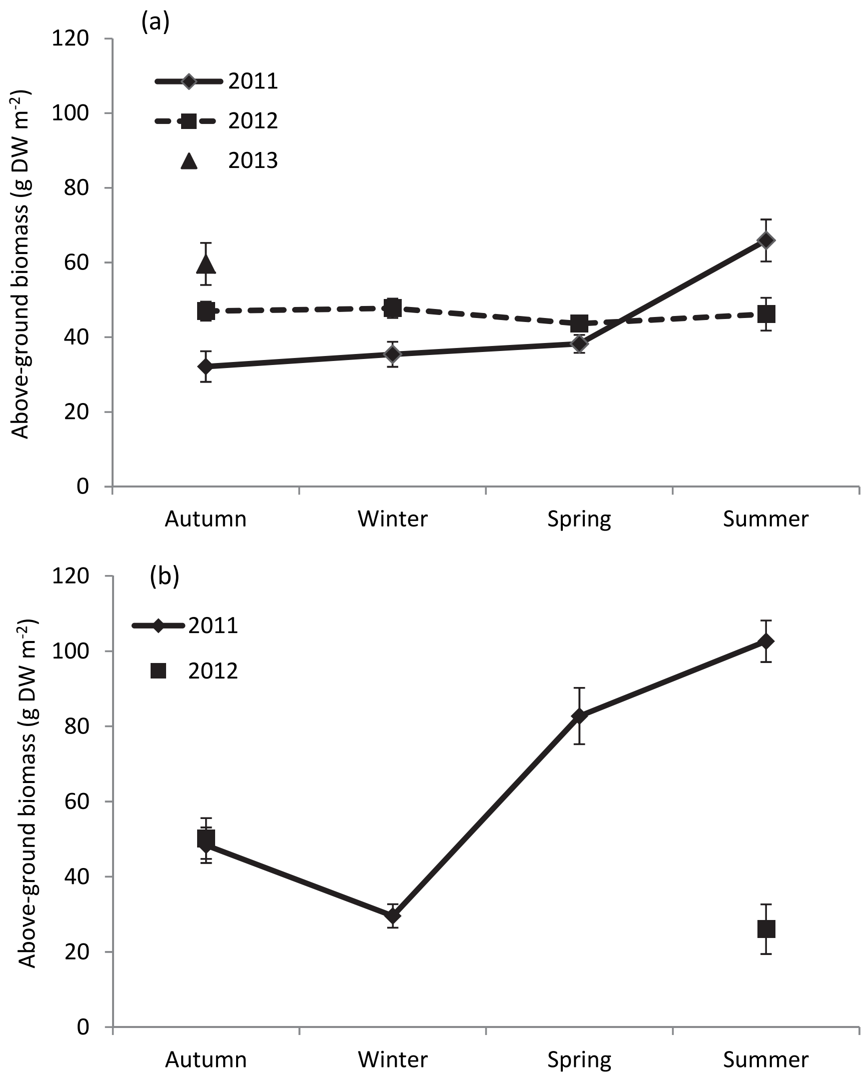


Figure 2. Average seagrass biomass (+ standard error) at (a) intertidal and (b) subtidal meadows, measured across four seasons and two full years (autumn 2011 – summer 2011/12 and autumn 2012 – summer 2012/13), and autumn 2013 (intertidal only).

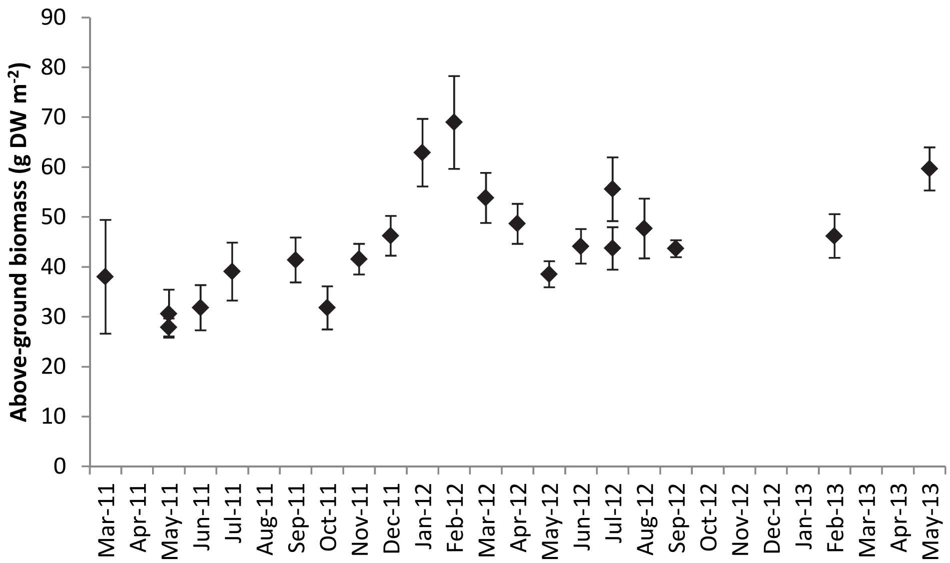


Figure 3. Above-ground biomass (+ standard error) of intertidal seagrass for each sampling period at Mabuiag Island, March 2011 – May 2013.

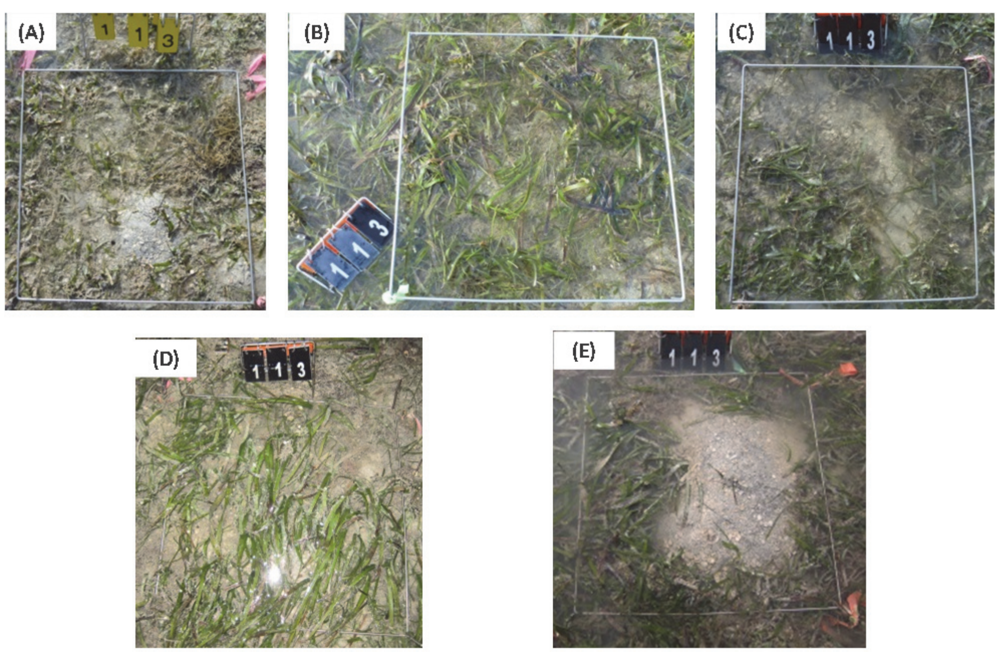


Plate 2. Seasonal and inter-annual variation in above-ground seagrass biomass in a permanent plot (A) May 2011, (B) February 2012, (C) May 2012, (D) February 2013 and (E) May 2013 at Mabuiag Island.

2.3.2 Environmental trends

Rainfall, global solar exposure and salinity

A distinct wet season (January – May; summer and autumn) and dry season (June – December; winter and spring) occurred in the Torres Strait during the study period (Figure 4). During the dry season little to no rainfall was recorded and salinity peaked (up to 41 ppt) (Figures 4, 5). During the wet season rainfall peaked (>100 mm) and salinity often fell below 32 ppt, particularly between February and April each year (Figures 4, 5). Global solar exposure was on average 21.5 $\pm$ 0.2 MJ m^{-2} day^{-1}. Global solar exposure peaked in late spring/ early summer (>30 MJ m^{-2} day^{-1}) and was lowest during peak rainfall periods during late summer (Figure 4). The lowest GSE measured was 1.9 (February 2012). Variation in GSE was greatest during the wet season.

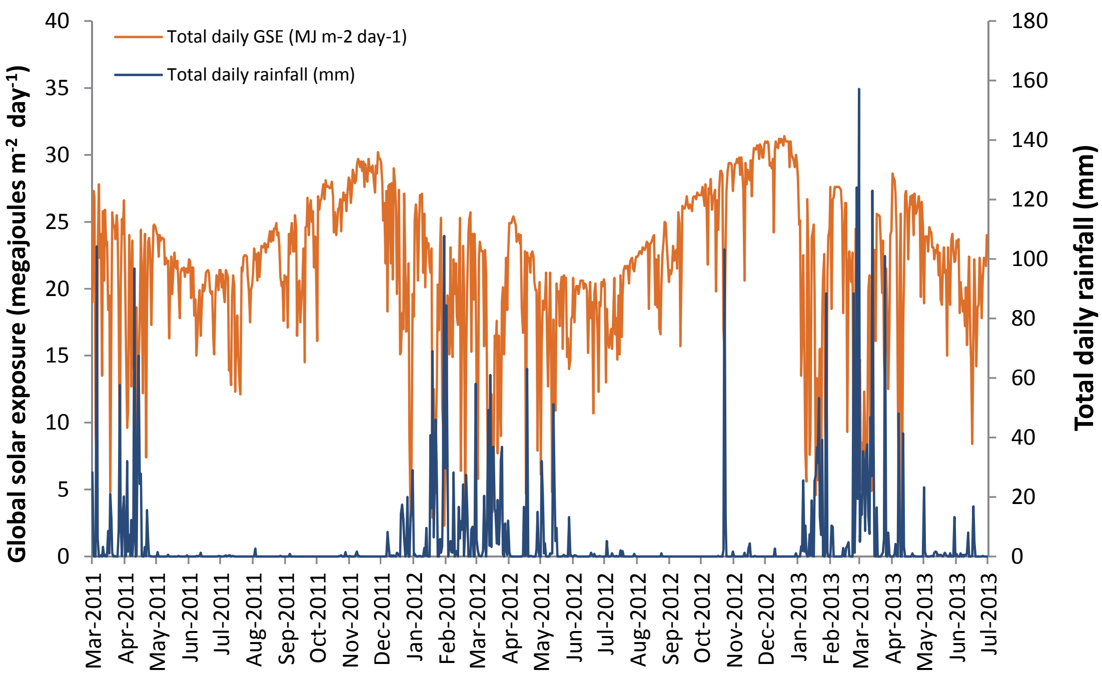


Figure 4. Daily global solar exposure (megajoules m^{-2} day^{-1}) and total daily rainfall (mm) at Horn Island, Torres Strait, March 2011 – July 2013.

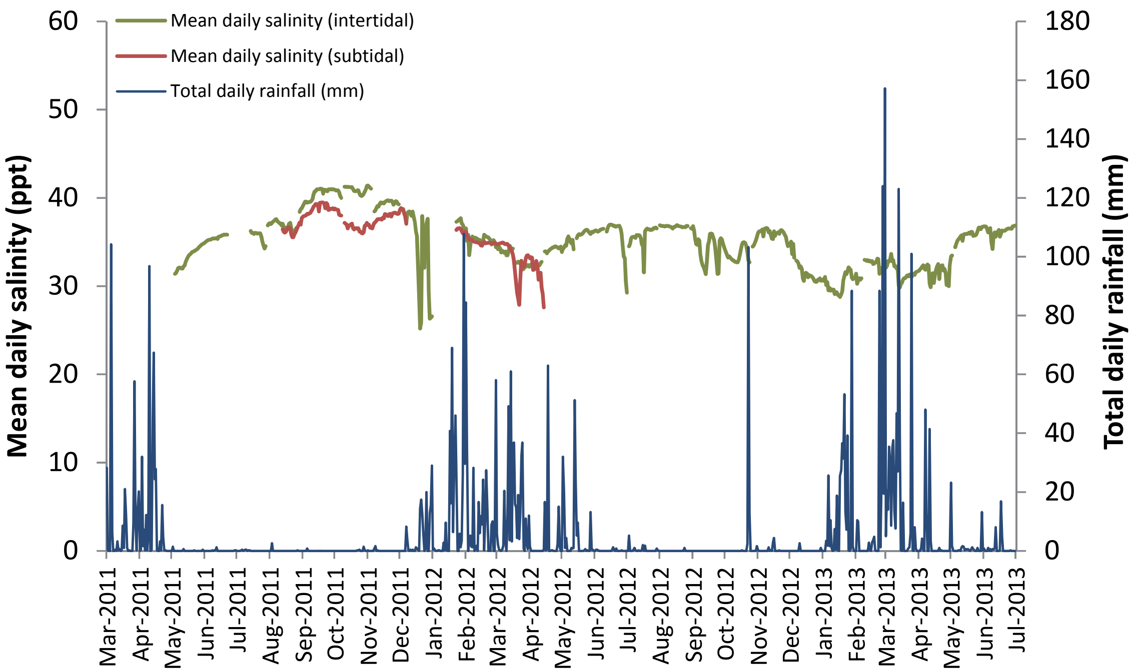


Figure 5. Mean daily salinity (parts per thousand, ppt) and total daily rainfall (mm) at intertidal and subtidal Mabuiag Island seagrass meadows, and total daily rainfall (mm) at Horn Island, Torres Strait, March 2011 – July 2013.

Tidal exposure

Intertidal seagrass meadows were exposed during daylight hours on low tide (1 - 7 days duration) for most spring tides during the sampling period. Exposure duration ranged between 30 minutes and three hours each day (Figure 6). Exposure peaked in terms of number of hours per day, and also the consecutive number of days, between August and October each year (late winter/ early spring). No daytime exposure was recorded between approximately November and early February each year (late spring/ summer).

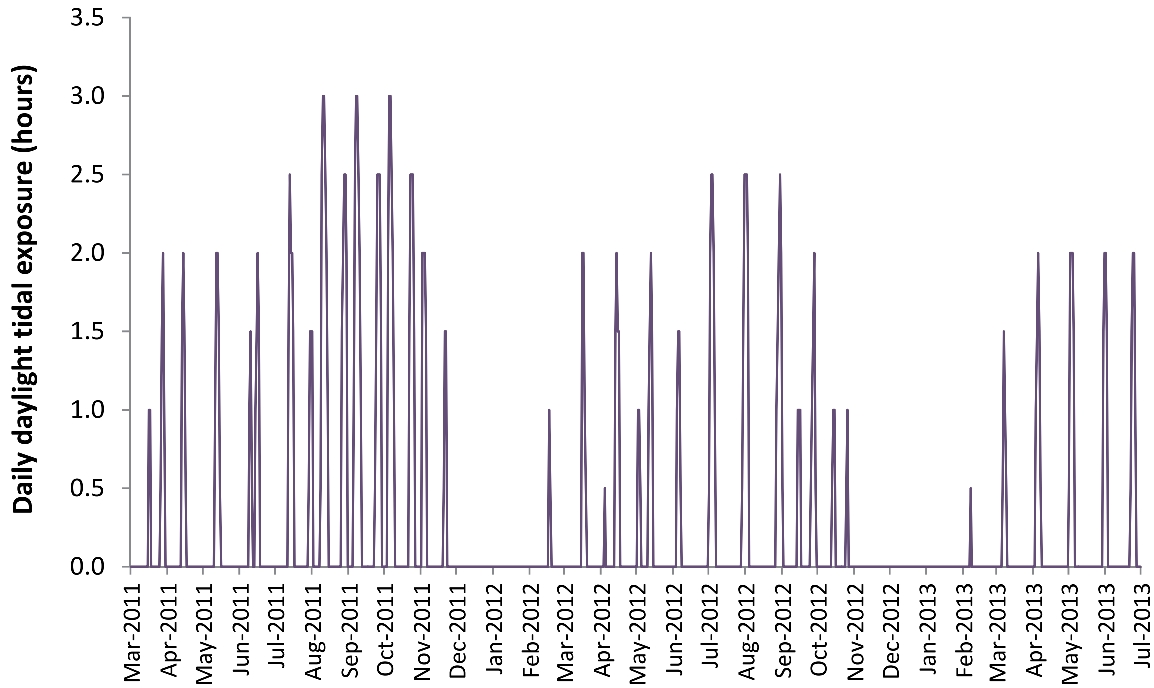


Figure 6. Total daily tidal exposure during daylight hours (0600-1800) at Mabuiag Island, Torres Strait, March 2011 – July 2013.

Photosynthetically active radiation (PAR)

The amount of photosynthetically active radiation (PAR) reaching intertidal and subtidal seagrass meadows, and therefore the light available for use in seagrass photosynthesis, was highly variable. Levels of PAR were highest during the dry season (June – December) when rainfall was lowest, GSE was highest and daytime tidal exposure was at a maximum (Figures 4, 6, 7). Intertidal meadows experienced approximately five times greater mean total daily PAR (15.4 $\pm$ 0.2 mol m^{-2} d^{-1}) compared with subtidal meadows PAR (2.9 $\pm$ 0.1 mol m^{-2} d^{-1}). Total daily PAR ranged from just under 1 mol m^{-2} d^{-1} to 39.0 mol m^{-2} d^{-1} in intertidal meadows, and between < 0.01 mol m^{-2} d^{-1} to 11.5 mol m^{-2} d^{-1} in subtidal meadows (Figure 7). The greater range in PAR at intertidal meadows was likely driven by tidal exposure. A low tide at midday, for example, would have left seagrass meadows (and PAR loggers) exposed during the time when sunlight was strongest, substantially increasing PAR. Conversely, on a midday high tide seagrass meadows (and PAR loggers) would have been completely submerged and PAR levels substantially reduced.

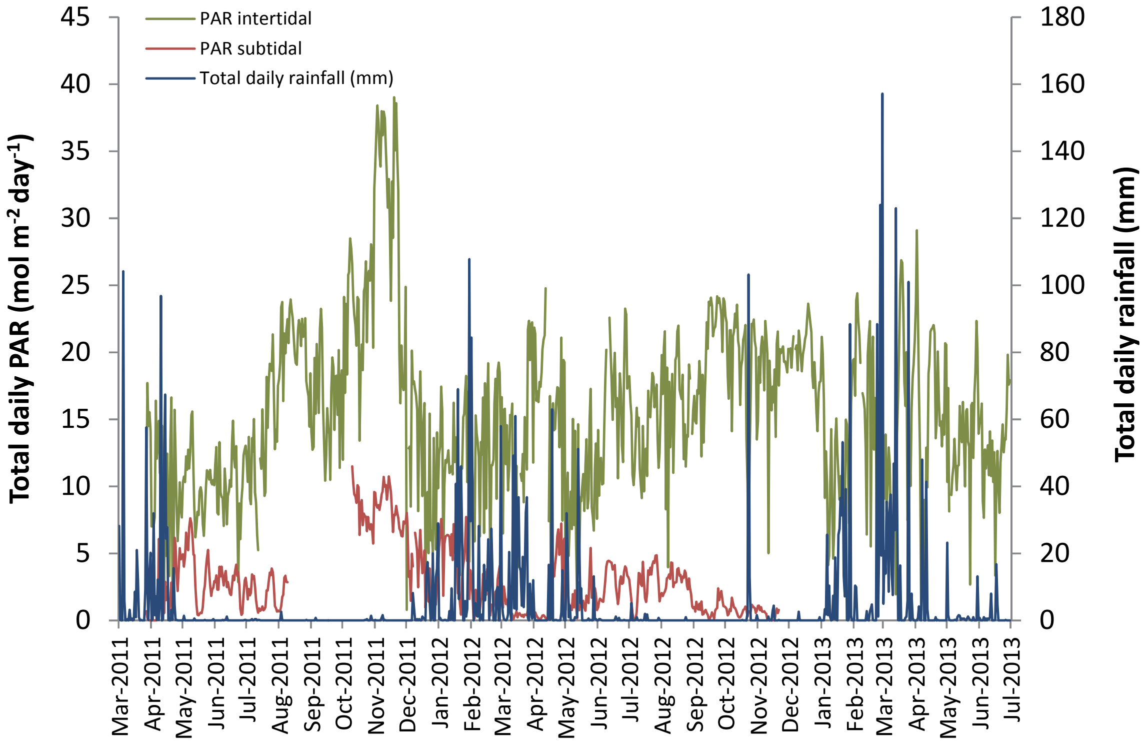


Figure 7. Total daily photosynthetically active radiation (PAR, mol m^{-2} day^{-1}) at intertidal and subtidal Mabuiag Island seagrass meadows, and total daily rainfall (mm) at Horn Island, Torres Strait, March 2011 – July 2013.

Water temperature

Mean daily water temperature in Mabuiag Island's intertidal meadows ranged from 24.1°C to 31.4°C, with an average of 27.8 $\pm$ 0.1°C (Figure 8). Maximum water temperatures (>35°C) were recorded mid-March to mid-April. The maximum water temperature recorded in the intertidal meadow was 4°C greater than in the subtidal meadow. Mean daily water temperature reached above 30°C only in the summer and early autumn (December - April), after which mean water temperature declined as expected with the transition from the hot wet season to the cooler dry season. The coldest mean daily water temperatures (<25°C) were recorded late July through to early September each year.

The range of mean daily water temperature in subtidal meadows was slightly less than intertidal meadows (24.6 - 31.0°C), with an average of 28.0 $\pm$ 0.1°C (Figure 8). Maximum daily water temperature (>31°C) and the highest mean daily water temperatures (>30°C) and were recorded in the summer and early autumn (December - April). Mean water temperature declined as expected with the transition from the hot months of the wet season to the cooler dry season. The coldest mean daily water temperatures (<25°C) were recorded late July through to early September. Interestingly, the mean daily water temperature in the subtidal meadow was very similar to that of the intertidal region, minus the sharp peaks observed in the intertidal zone during exposure times, despite being six metres below mean sea level (Figure 8).

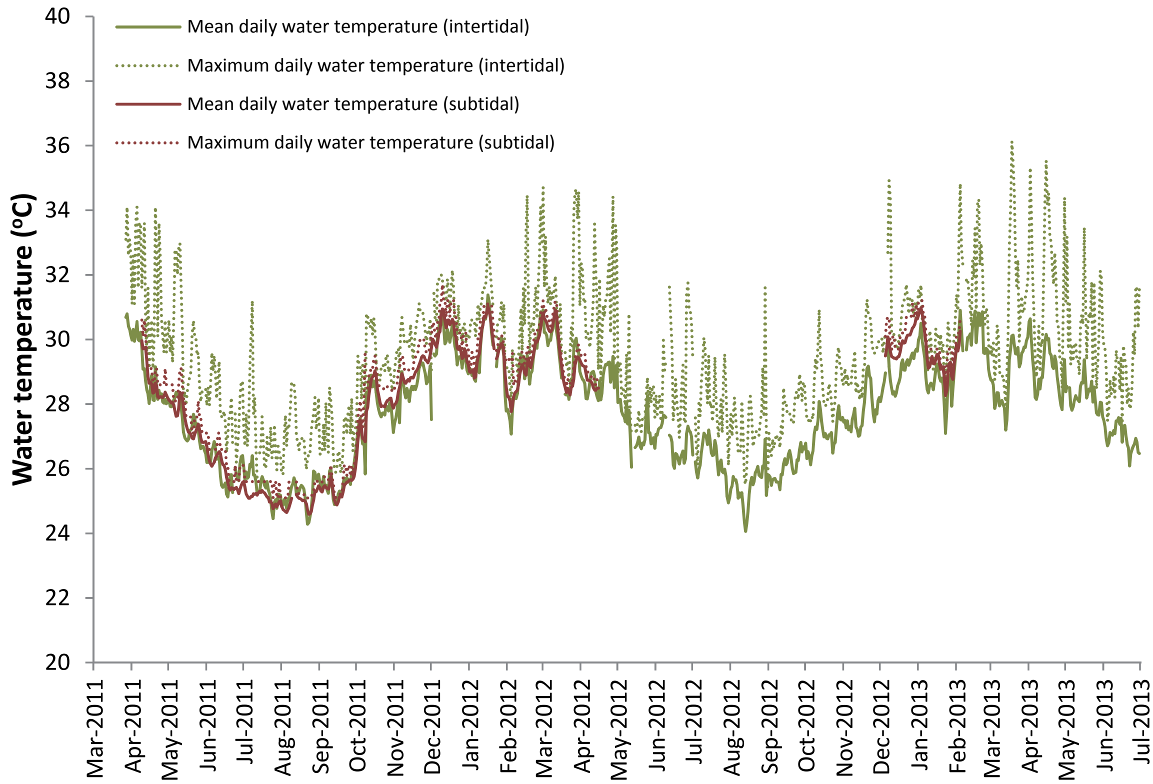
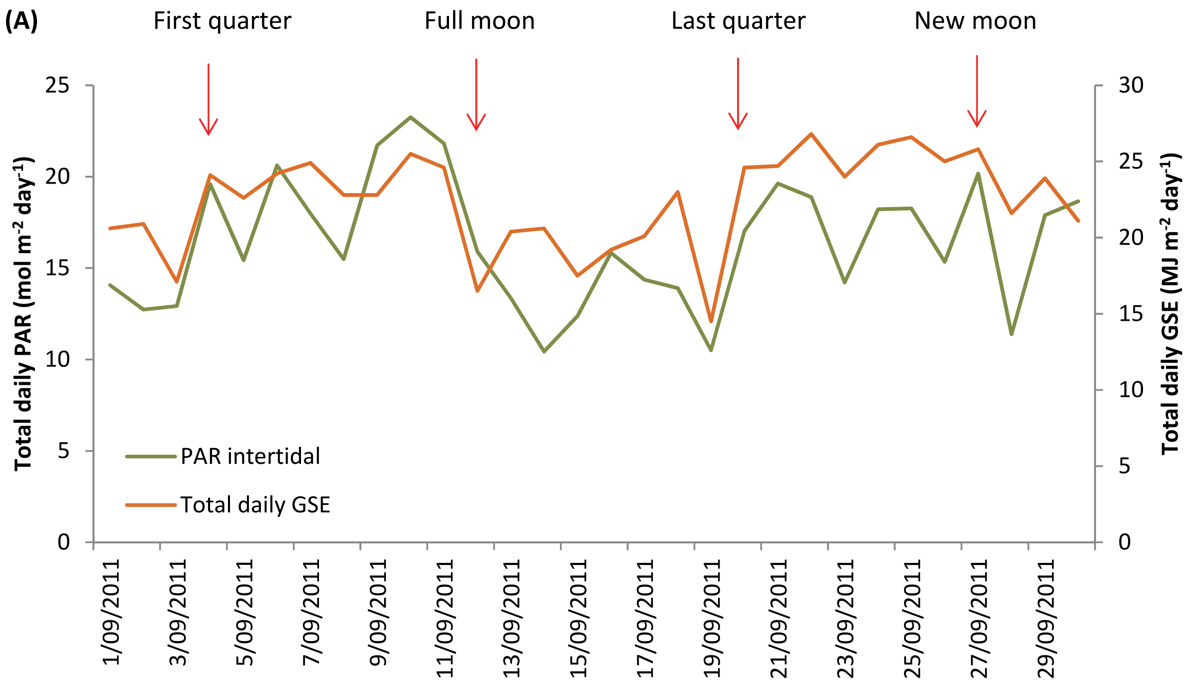


Figure 8. Mean (solid line) and maximum (dashed line) daily water temperature (°C) at intertidal and subtidal Mabuiag Island seagrass meadows, Torres Strait, March 2011 – July 2013.

Lunar cycles

Environmental conditions were also affected by lunar cycles, particularly in the intertidal meadow. During September 2011 there were fortnightly peaks in total daily PAR, total daily GSE, mean daily water temperature, and maximum daily water temperature. These peaks coincided with the lead up to the full moon and the time of the new moon when the tidal range was greatest and intertidal meadows experienced the highest levels of daytime tidal exposure (Figure 9).



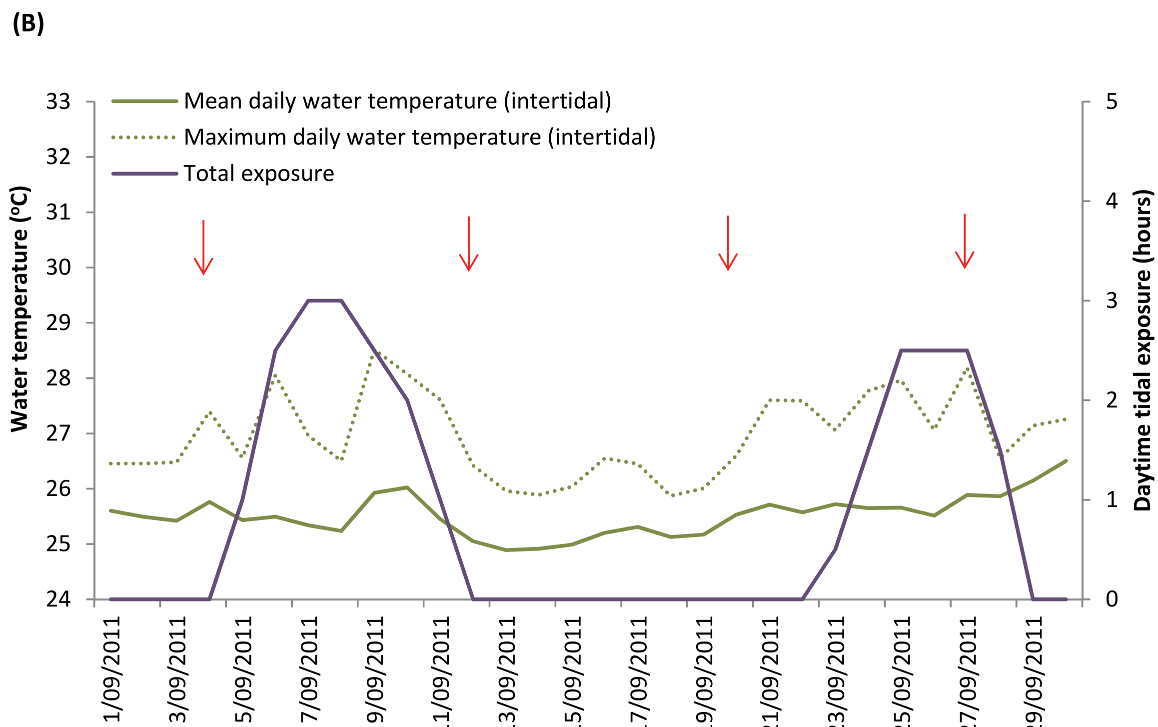


Figure 9. Daily variation in (A) photosynthetically active radiation (PAR, mol m^{-2} day^{-1}) and global solar exposure (GSE, megajoules m^{-2} day^{-1}); and (B) daily mean and maximum water temperature (°C) and daytime tidal exposure (hours) with lunar cycle at the intertidal seagrass meadow, Mabuiag Island, September 2011.

2.3.3 Environmental effects on seagrass biomass

Variation in above-ground seagrass biomass was best described by a model that included the terms for total daytime exposure (14d) and total rainfall (30d) (Table 2). High seagrass biomass values coincided with minimal total daytime tidal exposure in the 14 days prior to sampling (Figure 10a) and high total rainfall in the 30 days prior to sampling (Figure 10b).

Table 2. (A) AICc set of top models (AICc < 2) used for model averaging relating maximum water temperature (14d), total rainfall (30d) and total daytime tidal exposure (14d) to seagrass biomass in intertidal meadows at Mabuiag Island. (B) Standardized effect of factors on seagrass biomass after model averaging was performed on the top candidate model set for intertidal seagrass at Mabuiag Island.

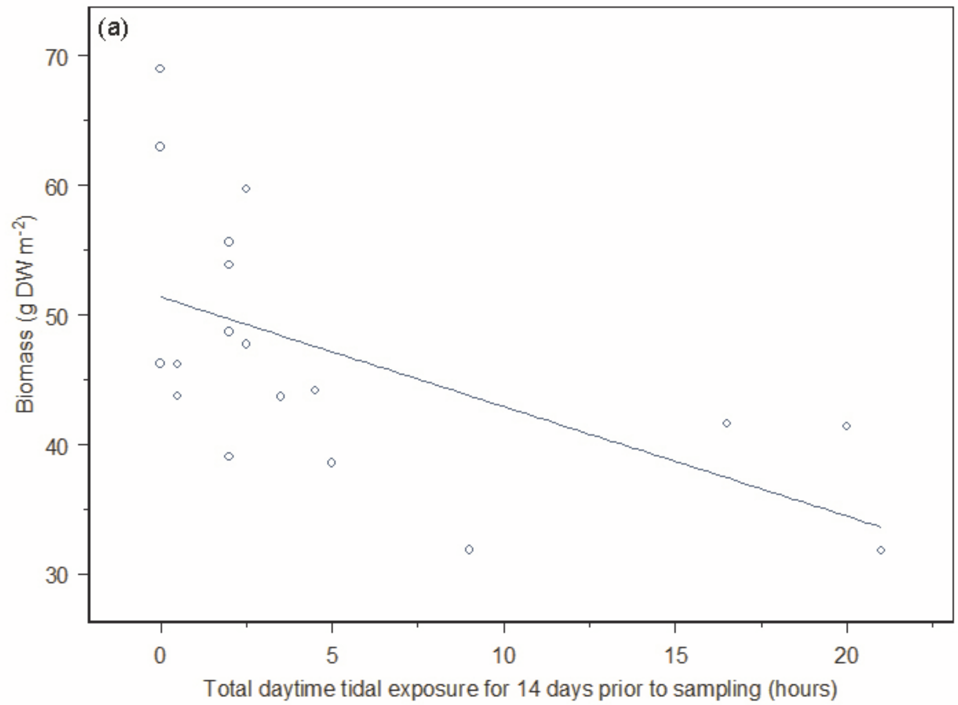
(A) Model	Coefficient (±95% CI)
Intercept	46.943 (43.064 ± 50.822)
Rainfall(30d)	12.380 (3.449 ± 21.312)
Exposure (14d)	-5.161 (-14.966 ± 4.645)

(B) Model	df	Log Lik	AICc	ΔAICc	w_i
Rainfall(30d)	3	-61.38	130.48	0.00	0.72
Rainfall(30d) + Exposure (14d)	4	-60.66	132.39	1.91	0.28

ΔAICc is the difference in AICc values between model *i* and the best model of those considered, and w_i is the probability that a model is the best model of the set.

Many of the environmental variables were correlated. Positive correlations were recorded between hours of tidal exposure and global solar exposure, tidal exposure and PAR, tidal exposure and salinity, and rainfall and salinity in intertidal meadows. Negative relationships between salinity and maximum and mean water temperature, tidal exposure and maximum and mean water temperature, tidal exposure and rainfall, rainfall and salinity, and rainfall and PAR were recorded (Figure 11, Appendix 1).

Scatter matrices for subtidal meadow biomass versus environmental variables showed indicated potential positive correlations between biomass and GSE, PAR and daytime tidal exposure (Appendix 2). This result should be taken with some caution as a lack of sampling events in the subtidal meadow meant that statistical verification of these apparent correlations was not possible.



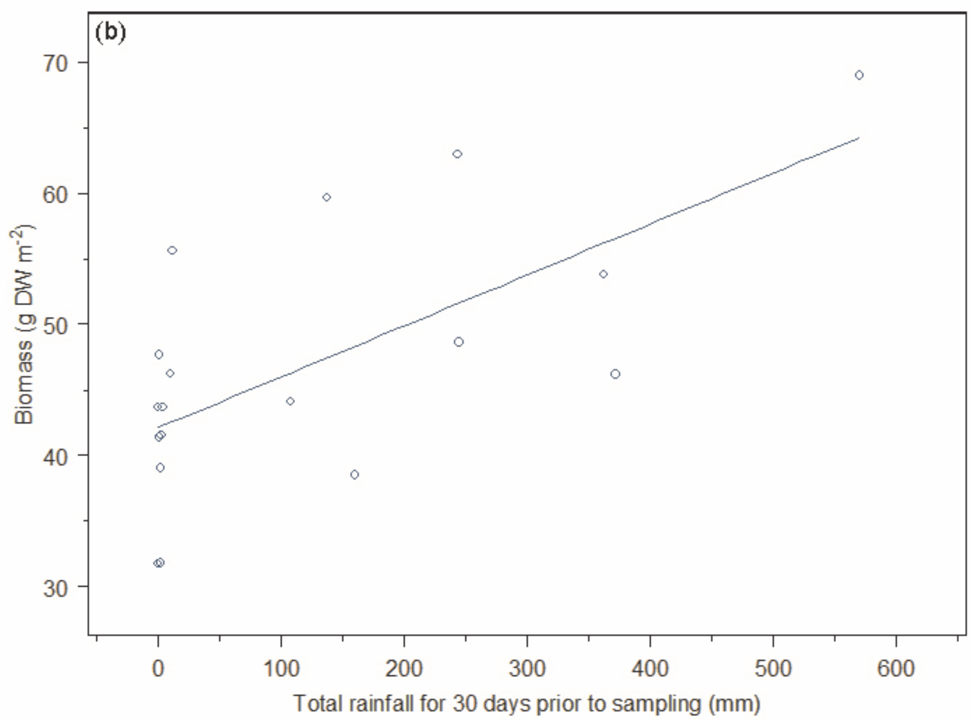


Figure 10. Relationships between (a) above-ground seagrass biomass and daytime tidal exposure 14 days prior to sampling (hours), and (b) above-ground seagrass biomass and total rainfall 30 days prior to sampling (mm) in the intertidal seagrass meadow.

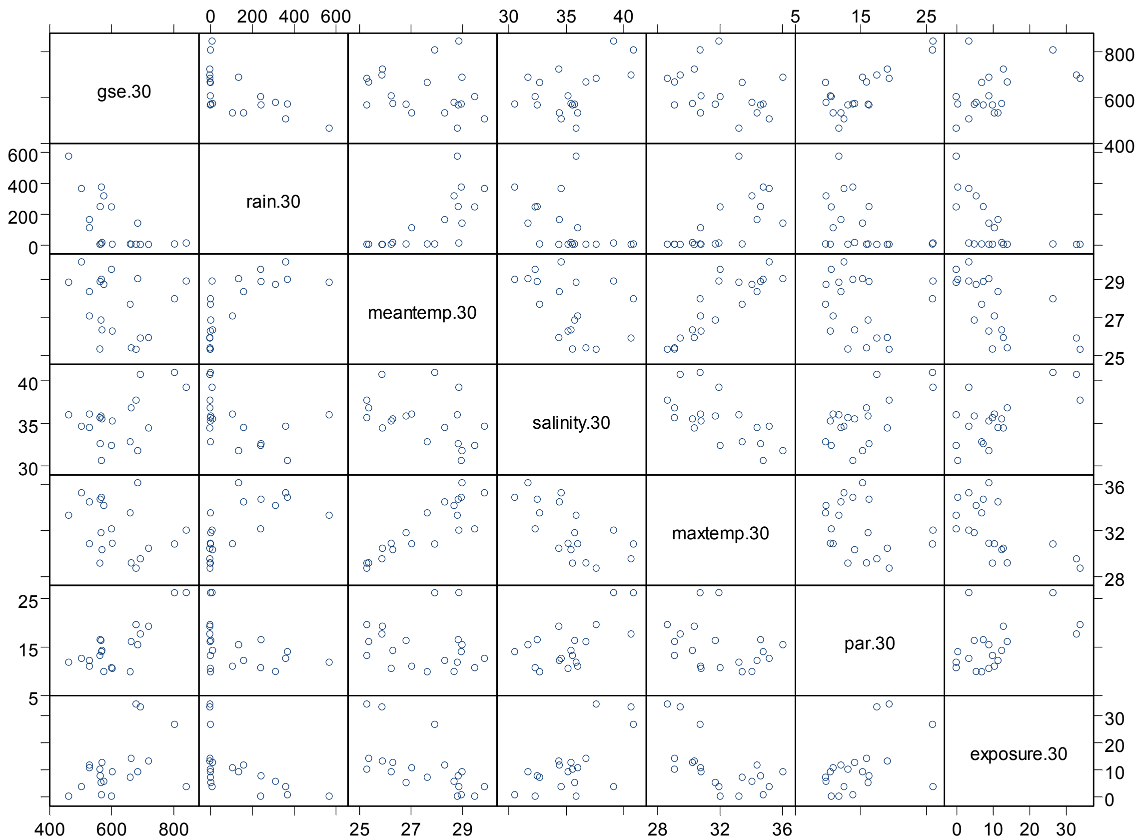


Figure 11. Scatter matrix of correlations between all environmental variables in the intertidal meadow in the 30 days prior to making estimates of seagrass biomass.

2.4 Discussion

Seagrass biomass at Mabuiag Island demonstrated distinct changes among years and among seasons. Changes in intertidal seagrass biomass were associated in particular with total daytime tidal exposure in the fortnight prior to sampling, and total rainfall in the month prior to sampling. Within the intertidal meadow correlations between daytime tidal exposure and salinity, for example, and rainfall and water temperature, indicate that a range of other environmental variables are likely to play some role in fluctuations in seagrass biomass. Statistical analysis of environmental effects on seagrass biomass in subtidal meadows was not possible, but a visual inspection of scatter matrices indicated that different environmental variables to those in intertidal meadows were likely drivers of biomass change, and that these were more closely linked with biomass peaking when light (GSE, PAR, and exposure) was at a maximum. This indicates that for subtidal seagrass light may be the limiting factor for growth. Further data collection is required, however, to confidently establish associations between subtidal seagrass dynamics and the environment, and to examine any potential interaction between season and year in seagrass biomass.

Changes in seagrass biomass between sampling times was greater than two-fold in the intertidal and four-fold in the subtidal meadows. Mabuiag Island subtidal and intertidal seagrass meadows exhibited a seasonal pattern in the first year of sampling where above-ground biomass reached maximum abundance in spring/summer and a minimum in autumn/winter. In the second year of sampling, however, seasonal variation was not as strong and biomass was greatest in autumn/winter. This pattern was consistent among intertidal and subtidal meadows. Seasonality in seagrass biomass varies from little effect (e.g. Hillman et al. 1989; Brouns 1987; Brouns 1985) to a significant effect of season (Rasheed et al. 2008). At the nearby

Orman Reefs in Torres Strait biomass and growth of similar multi-species seagrass meadows varied by up to a factor of 3.5 during one year (Rasheed et al. 2008) while in South East Asia seagrass biomass varied by a factor of four (Lanyon and Marsh 1995; Erftemeijer and Herman 1994).

Mabuiag Island's intertidal seagrass biomass was at its greatest when rainfall was high. This may appear counter-intuitive considering seagrass biomass decreased in intertidal meadows from late summer and through autumn in 2011 and 2012 when rainfall peaked. The greatest biomass in intertidal meadows (69 $\pm$ 9 g DW m^{-2} in February 2012) was recorded, however, following the month of heaviest total rainfall on record during this study (570 mm), and similar high biomass periods were recorded after heavy rainfall in March 2012 and May 2013. The Mabuiag Island region lacks large river systems, indicating increased rainfall does not lead to the large, freshwater pulses that seagrass meadows experience on Australia's east coast that can lower salinity and light levels to the point where seagrass growth is negatively impacted (Campbell and McKenzie 2004). The positive influence of rainfall on seagrass change is most likely driven by run-off and river flow during rain events of a small enough magnitude where seagrasses receive an increase in nutrients favourable for growth (e.g. Rasheed and Unsworth 2011), but not so much run-off that salinity and light is so reduced that growth is adversely affected. Studies conducted on a limited number of seagrass species suggest most species have optimal growth when salinity ranges from 30 - 40 ppt (Touchette 2007; Kahn and Durako 2006). Salinity decreased with rainfall at Mabuiag Island (Figure 5) but, despite short-term peaks and troughs outside of the 30 - 40 ppt range mean salinity during peak rainfall months in late summer/ autumn, salinity ranged from 30.5 - 35.9 ppt in the month prior to sampling, well within the range for optimal growth.

Seagrass biomass was negatively affected by daytime tidal exposure in the two weeks prior to sampling in the intertidal meadow. Periods of no exposure occurred during December 2011 – February 2012, and December 2012 – January 2013. During the last month of the 2011-2012 period of no exposure seagrass biomass peaked above 60 g DW m^{-2}. Unfortunately no sampling occurred during the no exposure period in 2012-13 to demonstrate whether the effect of no exposure was consistent among years. Sampling over the 2013-2014 no exposure period will strengthen our model in relation to the effects of exposure on seagrass biomass. The negative effect of daytime tidal exposure on meadow biomass was most likely due to intense midday insolation and, when seagrasses became fully exposed, severe desiccation and 'burning' (i.e. browning of the leaf material). Burning was observed regularly in the intertidal region, particularly for *Enhalus acoroides* during the spring months when hours of exposure and light levels (PAR) were greatest. Other studies of Indo-Pacific and north Queensland intertidal seagrass meadows have found that long and frequent periods of tidal exposure during the day can result in desiccation, temperature and high light stress, leading to permanent morphological and physiological damage to the plant (Unsworth et al. 2012; Stapel 1997; Erftemeijer and Herman 1994). The mechanisms by which exposure leads to seagrass decline are likely related to physiological stress to the leaf structure and photosystems, probably through excess light causing photo damage (Kahn and Durako 2006; Bjork et al. 1999). This occurs when excess irradiance causes the production of oxygen-free radicals, which in turn damages the photosynthetic apparatus (Demmig-Adams et al. 2004). It is noteworthy that during the months where exposure occurs (March to November each year) biomass ranged from 28 $\pm$ 2 to 42 $\pm$ 3 g DW m^{-2} in 2011, a year with relatively high daytime tidal exposure, compared to a much greater biomass range of 38 $\pm$ 3 to 56 $\pm$ 6 g DW m^{-2} in 2012 when exposure was relatively lower (Figure 6).

Seagrass biomass was also at a maximum when water temperature peaked during summer, with the positive correlation between rainfall and water temperature indicative of the summer monsoon (Figure 11). Water temperature significantly affects the biochemical processes involved in photosynthesis and respiration and has long been considered a major factor controlling seasonal seagrass growth (Lee et al. 2005; Lee and Dunton 1996; Phillips et al. 1983; Tutin 1942). Leaf productivities (growth) of many tropical seagrass species increase with increasing water temperatures (from 23°C to 29°C) (Lee et al. 2007; Lee and Dunton 1996). Average daily water temperatures at Mabuiag Island were within this optimal range for tropical seagrass growth with the exception of summer/ early autumn, when mean and maximum water temperatures were often >30°C (Figure 8). Inhibition of growth has been recorded when temperatures reach a threshold of >35°C and thermally-induced physiological stress occurs (Campbell et al. 2006; Ralph 1998a; Bulthuis 1983). Water temperatures recorded at Mabuiag Island suggests seagrasses in this region may be living at their thermal maximum. This is of concern given the expected future climate scenarios of increased sea surface temperatures (Australian Bureau of Meteorology and CSIRO 2011) as any increase in water temperature may have a deleterious impact on the productivity of this shallow water ecosystem. Maximum water temperature at Mabuiag Island did spike above 35°C, although these spikes generally occurred March through May when mean water temperature was declining which may have shielded the plants to some extent from physiological stress (Figure 8). Spikes in water temperature corresponded with the commencement of periods of daytime tidal exposure and a decline in seagrass biomass, indicative of “super-heating” of the thin layer of water covering intertidal meadows during low tide events. Temperatures in excess of 40°C have been commonly observed in *Halodule uninervis* seagrass meadows throughout Queensland (McKenzie and Unsworth 2009), although only one spike >40°C was recorded at Mabuiag Island (in March 2011). Manipulative studies to determine the thermal maximum of seagrasses in the Mabuiag Island region are warranted.

Photosynthetically active radiation levels showed expected responses to weather and tidal patterns. During periods of heavy rainfall, PAR decreased in both the intertidal and subtidal meadows, likely due to a high percentage of cloud cover lowering atmospheric PAR (Figure 7). Peaks in intertidal PAR also coincided with daytime tidal exposure. The growth, survival and depth penetration of seagrass is directly related to the quality and quantity of light (Dennison 1987; Dennison and Alberte 1985), which is the primary driver of photosynthesis. The lack of a significant relationship between seagrass biomass and PAR indicate that seagrasses at Mabuiag Island are likely receiving greater than their minimum light requirements. Recent studies in Gladstone have demonstrated that intertidal *Zostera capricorni* relies on greater than 6 mol m^{-2} d^{-1} over a two week rolling average of light during the growing season (July – January for Gladstone seagrasses) to remain stable or increase in abundance (Chartrand et al. 2012). Collier et al. (2012) similarly reported that *Halodule uninervis* at three island locations in the northern Great Barrier Reef required between 5 and 8.4 mol m^{-2} d^{-1} for growth. Intertidal light levels at Mabuiag were highly variable, but PAR rarely fell below 5 mol m^{-2} d^{-1} and the range in mean daily PAR was generally 5-15 mol m^{-2} d^{-1} during the summer wet season and 20-25 mol m^{-2} d^{-1} during the dry season (Figure 7). Light levels at Mabuiag’s intertidal meadow are therefore likely to be in excess of the minimum requirements of most tropical seagrass species.

Seasonal and inter-annual observations of seagrass meadow biomass at Mabuiag Island have so far only been conducted over two seasonal cycles, a relatively short timeframe for climate studies. Considering the differences among seasons and years in seagrass biomass and environmental conditions, continued seasonal monitoring in 2013-2014 will substantially improve our understanding of the range of natural seasonal change and relationships between seagrass biomass and the environmental conditions meadows experience.

3 CAPACITY FOR SEAGRASS RECOVERY

3.1 Introduction

Physical loss of seagrass occurs due to many types of physical disturbances such as storms (Poiner et al. 1989), grazing - particularly by dugong (Preen 1995), anchor and boat damage (Williams 1988; Zieman 1976) and shipping accidents (Kenworthy et al. 1993). In the Torres Strait, the threat of seagrass loss due to shipping accidents may be considerable given that one of the most heavily used shipping lanes in Australia transits the region. The Great North East (GNE) Shipping Channel connects the eastern seaboard of Australia with many Asian countries to the north, including China. Approximately 3000 voyages are undertaken by shipping vessels (bulk tankers) through the GNE channel each year (Neil Trainor, AMSA, pers. comm. 2008). Heavy reliance of Australian trade industries on export and import means the level of use of the GNE Channel is expected to rise by 20% in the next five years (AMSA 2011). The Torres Strait region has a high rate of shipping incidents compared to other shipping passages. There are at least 20 separate accidents recorded back to 1970, 18 of which were ship groundings on reefs, with the remaining two being discharge accidents while docked at the Port of Thursday Island (Queensland Transport and GBRMPA 2000).

A key aspect in understanding the resilience of seagrass meadows to stressors is their capacity to recover from impact (Kenworthy 2000). The responses of seagrasses to removal-related disturbance have been assessed through both experimental and descriptive studies, highlighting the different responses of seagrass communities following loss, and the importance of reproductive strategy to the recovery of gaps. Gaps in *Halodule uninervis* meadows recovered within four months at Abbot Point, Queensland (Unsworth et al. 2010) while recovery at Green Island, Queensland, required seven months (Rasheed 2004). Seagrass communities dominated by relatively larger, slower growing species (i.e. *Enhalus acoroides, Cymodocea* spp.) have been reported to take over five years to recover from disturbances (Rollón et al. 1999).

Seagrasses may colonise cleared patches by dispersal of sexual propagules (seeds, fruits, flowers) and/or asexual vegetative extension of plants at the periphery and replacement of above-ground structures (Rasheed 2004; Rasheed 1999; Rollón et al. 1999). Differences in the means of recovery (asexual vs. sexual) between species may also be an important factor in determining the sequence in which individual species return to disturbed patches. Means of recovery are also likely to play a role in recovery rates in small versus large scale disturbances. In larger scale disturbances where few remnant plants remain, initial colonisation can occur by seeds or other sexual propagules (Duarte and Sand-Jensen 1990; Phillips et al. 1983). Subsequent development of seagrass patches may then depend on asexual reproduction (Duarte and Sand-Jensen 1990).

With increasing levels of shipping activity in the Torres Strait and the associated threat of negative effects on seagrass communities, an understanding of the recovery process is essential in developing strategies to deal with potential disturbance. Information on how seagrass systems naturally recover is likely to be useful in attempts to artificially rehabilitate seagrasses, which have met with mixed success in the past (Thorhaug and Cruz 1988; Phillips 1982; Thorhaug and Austin 1976), and in developing management plans where seagrasses are highly impacted.

The goals of this study were to:

1. Determine the capacity for, and the rate of recovery of Torres Strait seagrasses;
2. Identify the roles of sexual versus asexual reproduction;
3. Establish whether seasonality of seagrass abundance affects recovery rates; and
4. Ascertain patterns of succession of seagrass species following artificial disturbance in a mixed species meadow

3.2 Methods

3.2.1 Seagrass recovery following disturbance

The rate of seagrass recovery, the role of sexual and asexual reproduction, and the species involved in re-colonisation following loss/removal were investigated at the two experimental locations. These investigations followed the methods developed for investigating seagrass recovery after loss/removal (Unsworth et al. 2010; Rasheed 2004; Rasheed 1999). At each location, three experimental blocks were subject to a randomised block design of 12 (0.25 m^2) treatment plots of seagrass. Within each block, the 12 plots were subject to three replicates of four different treatments (Table 3).

Table 3 Description of treatments for re-colonisation experiments.

Treatment	Cleared	Not Cleared	Bordered	Not Bordered	Replicates
C1		✓		✓	3
C2		✓	✓		3
E1	✓		✓		3
E2	✓			✓	3

Within each block, six of the 0.25 m^2 plots of seagrass had seagrass material, including roots and rhizomes, removed. Half (three) of the cleared plots in each block had an aluminium border sunk 500mm into the sediment to determine how recolonisation was influenced by asexual reproduction (seagrass runners). The border isolated treatments from asexual colonisation by stopping rhizome extension from seagrass surrounding the plots. To investigate how recolonisation was influenced by the availability of sexual propagules (seeds), recovery of seagrass was compared among plots that had all material removed but the seed bank left intact. Recolonisation of all the cleared plots were compared monthly to control plots in each block that was left undisturbed. Seagrass recovery and re-growth from each individual 0.25 m^2 plot was measured using non-destructive techniques including leaf shoot density and visual estimates of above-ground biomass (Rasheed 2004; Rasheed 1999; Mellors 1991). The number of flowering and fruiting bodies of each seagrass species present in the plots was also counted by observers.

Manipulative seagrass experiments were set up in the seagrass senescent season March/April 2011 in one subtidal and one intertidal location. A second round of recovery experiments was established in the seagrass growing season in late August 2011 (intertidal) and early November 2011 (subtidal) to determine if recovery of seagrasses were affected by seasonal change. The intertidal blocks for both rounds one and two were sampled monthly on a spring low tide, until September 2012 when sampling was altered to quarterly. Unfortunately, consistently poor weather meant that the subtidal blocks had only been re-sampled intermittently when the weather allowed. Results for both intertidal and subtidal sampling up to twenty five months post clearing for round one and approximately twenty months post clearing for round two are presented here.

3.2.2 Seagrass reproductive assessment

Seagrass reproductive health was assessed quarterly by taking 12 randomly placed cores (100mm diameter and depth) from an area adjacent to experimental locations and frozen for transport to the laboratory. The density of seeds in the meadow (seeds m^{-2}) was determined from the average number of seeds per core. Cores were sieved through a series of sieves between 4mm - 250µm to separate out the seagrass and reproductive material from the sediment. In the > 710 µm size fraction of the sediment, reproductive structures (male and female flowers, spathes, fruits and seeds) were identified and counted. Furthermore, the 250-710 µm fraction was inspected using a dissecting microscope to find the much smaller *Halophila* seeds. In addition, seagrass reproductive structures (flowers and fruits) for each species were counted within seed cores and recorded in the experimental plots (see part A above) during sampling events for the seagrass recovery experiments. Densities of flowers and fruits were only determined using the two control treatments to ensure that the data was not skewed by lower shoot presence in cleared treatments.

3.3 Results

3.3.1 Seagrass recovery following disturbance

The role of sexual and asexual reproduction (seeds versus runners) was a major factor in the recovery of cleared experimental plots (Figures 12 – 14). In general, preventing asexual colonisation (bordering) had a significant impact on the rate at which cleared plots recovered in relation to control plots in both the intertidal and subtidal. Up to 25.5 months after clearing, no bordered plots had recovered to control levels of above-ground biomass in the intertidal. In contrast, where asexual colonisation was permitted, seagrass above-ground biomass had recovered within 6 - 8 months, although species composition of seagrasses in the intertidal took a much longer time to return to the undisturbed state. It was not until 22.5 months post clearing (Round 1) that the species composition in cleared, non-bordered treatments was similar to that of corresponding controls.

There were strong differences in recovery times between intertidal and subtidal seagrasses. Initial recovery of seagrass into cleared plots was generally much slower for subtidal than for intertidal seagrasses. Subtidal seagrass biomass was similar in cleared, non-bordered plots from 12 months, approximately 4 - 6 months later than for intertidal seagrass (Figures 12 and 14; Appendix 3 and 4). Species composition in the subtidal returned to normal, however, at the same time, likely as a consequence of the dominance of pioneering, fast growing seagrass species. Seagrass biomass returned to the undisturbed state for cleared, bordered treatments during the study (after 20 months), which did not occur for this treatment in the intertidal meadow, however subtidal species composition still differed. The presence of a border did not have an impact on biomass of established seagrass in control treatments intertidally or subtidally (Figures 12 and 14; Appendix 3 and 4).

Timing of disturbance to seagrasses had little effect on recovery rates. Seagrasses in the cleared treatments from the second round of experiments which were set up near the beginning of the seagrass growing season recovered slower than those cleared in the senescent season in Round 1.

Intertidal recovery

Initial recolonisation in the intertidal cleared plots was observed from as early as one month after clearing (Figures 12 and 13). When recovery was able to occur through asexual means (no border), seagrass shoot density and above-ground biomass was significantly higher than in bordered plots which relied on sexual means from as early as 2 - 3 months post clearing. At the last sampling event for Round 1 (25.5 months after clearing), treatments that had been cleared and which were surrounded by a border (preventing asexual recolonisation) had significantly lower above-ground biomass than treatments that were cleared and not enclosed by a border. However, for Round 2 the two cleared treatments were not significantly different at the final sample (21 months after clearing Round 2), although biomass in the bordered treatment was still lower.

Above-ground biomass in treatments that could be colonised asexually (cleared, no border) recovered to the same density as undisturbed controls 5.5 months after clearing for Round 1 plots (September 2011) and

8 months for Round 2 plots (April 2012) and remained at the same levels as controls until May 2013 (Figure 12; Appendix 3 and 4). In these same treatments (cleared, no border) shoot density recovered to undisturbed levels 5.5 and 7 months (Rounds 1 and 2 respectively) after clearing (Figure 12; Appendix 3 and 4).

Where recovery was dependent on sexual means (i.e. recovery from seed bank or seed recruitment; bordered), seagrass demonstrated little recovery up to 18 months post-clearing, followed by a steady increase in biomass driven by increases in *Halodule uninervis* and *Cymodocea serrulata* (Figure 13). Above-ground biomass of these treatment plots reached 77% of control plot biomass at 25.5 months after clearing for Round 1 and 54% at 21 months for Round 2 of the experiment. Shoot density in the cleared, bordered treatments recovered much faster, reaching a similar density to control plots (approximately 75% and 50% of control plot shoot density) at 15 months and at 10.75 months (Rounds 1 and 2 respectively) although reflecting a different species composition (smaller species) recruiting into these treatments.

Shoot density and above-ground biomass varied seasonally (see section 1 above) in the control treatments for both rounds of experiments with spring/summer highs and winter lows, although the seasonal trend was not as strong in 2012-2013 as it was in 2011-2012 (Figure 12). Periods of decline in shoot density and biomass for cleared, no border treatments coincided with the lows in the uncleared control treatments (Figure 12).

The most dominant species in the uncleared controls for the intertidal sites by shoot count were *Halodule uninervis* and *Syringodium isoetifolium*, accouting for between 25-55% of the species composition each throughout the 25.5 months of the study. The species composition in treatments where asexual colonisation could occur (non-bordered) remained different to uncleared controls throughout the study despite total shoot density recovering to the level of uncleared controls. Overall, these treatments had reduced levels of *Thalassia hemprichii* (Figure 13).

Halodule uninervis was the most rapid asexual coloniser, dominating recovery of seagrass in non-bordered treatments. *Cymodocea serrulata, Halophila ovalis* and *Syringodium isoetifolium* also played a role in early recolonisation into non-bordered treatments (Figure 13). Densities of *Cymodocea serrulata, Cymodocea rotundata, Syringodium isoetifolium* and *Halophila ovalis* approached undisturbed levels 5 - 7 months post clearing.

Densities of *Halodule uninervis* remained lower than uncleared controls until 5 - 9 months (Rounds 1 and 2) after clearing when densities became considerably higher than in corresponding controls (Figure 13). This remained the case until 18.5 months post clearing (Round 1) when *Halodule uninervis* densities reduced to be in line with corresponding controls. Twenty-one months post clearing in Round 2 *Halodule uninervis* levels were still elevated and accounted for 70% of the species composition in cleared, non-bordered treatments as opposed to 51% in corresponding uncleared controls.

Thalassia hemprichii was the seagrass species that showed the slowest recovery rates into cleared non-bordered plots. Low counts of shoots were first identified approximately 5.5 - 6 months post clearing (Rounds 1 and 2), however it was not until 22.5 months (Round 1) that densities overlapped with those of corresponding controls. After 21 months for Round 2, *Thalassia hemprichii* shoot counts were still far reduced compared with corresponding controls (Figure 13).

Recovery of seagrass into plots where asexual colonisation was prevented by a border was almost solely by *Halodule uninervis*. *Halodule uninervis* first appeared in these plots three months post clearing and remained the dominant species (by shoot count) up to 25.5 months post clearing (Figure 10). Shoots of *Cymodocea serrulata, Thalassia hemprichii, Cymodocea rotundata, Enhalus acoroides* and *Halophila ovalis* had been recorded intermittently in cleared, bordered plots from five months post clearing, however most of these did not persist. The exception was *Cymodocea serrulata* which steadily increased in density (shoot count) from 16.5 months post clearing (Round 1). Recovery may have been by seed germination or from settling of vegetative fragments (Figure 13).

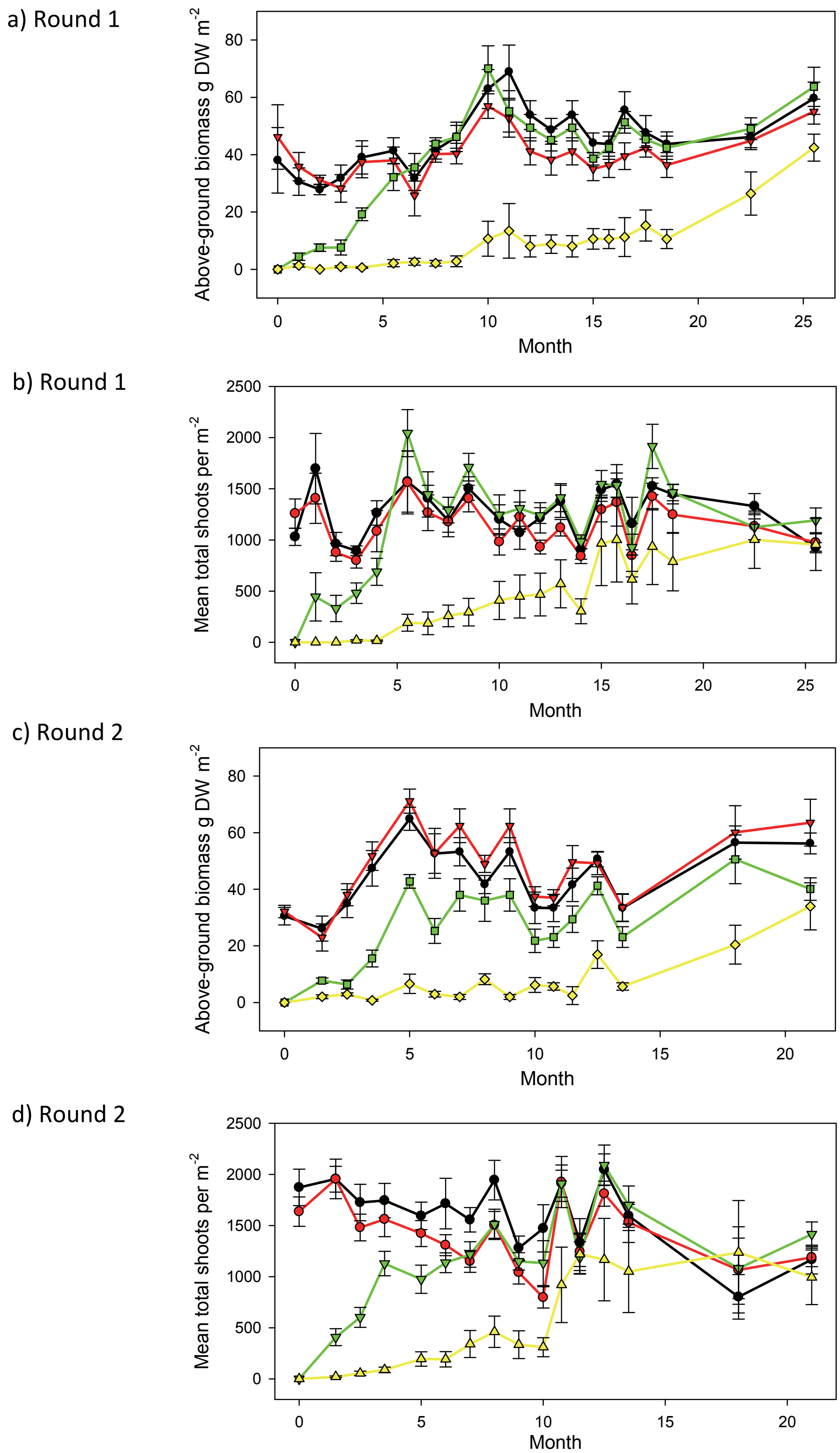


Figure 12. Mean above-ground biomass ± standard error (g DW m^{-2}) and mean total shoot density ± standard error (shoots m^{-2}) for each treatment in Round 1 (a, b) and Round 2 (c, d) in the intertidal region. Control, no border (black); control, border (red); cleared, no border (green); border (yellow).

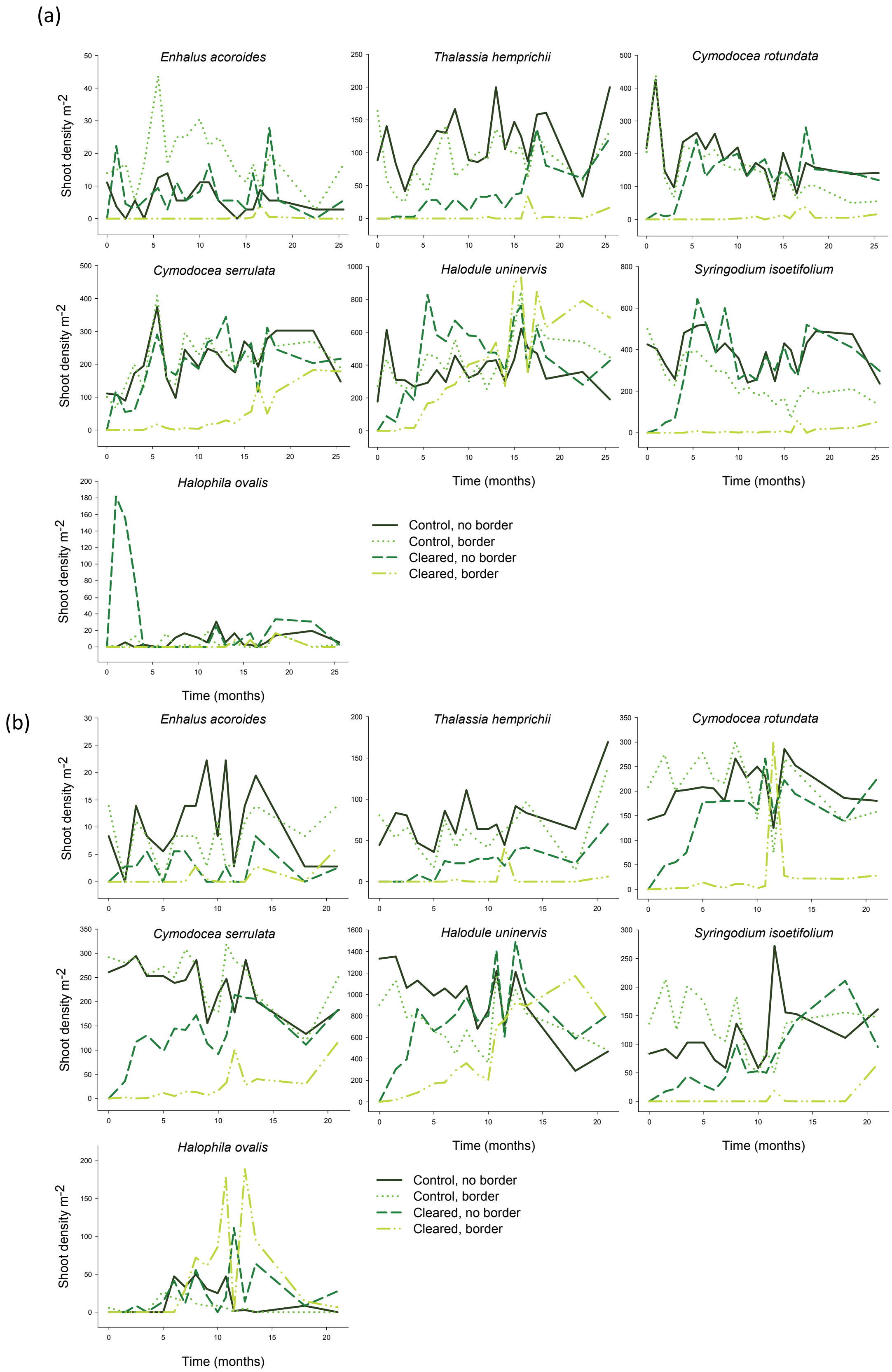


Figure 13. Mean shoot density (shoots m^{-2}) by species for each treatment in the intertidal region for (a) Round 1 and (b) Round 2.

Subtidal recovery

In the subtidal region seagrass recovery into cleared treatments was slower than that observed in the intertidal. Initial recolonisation was recorded in the cleared plots from as early as one month after clearing occurred (Figure 14 and 15). Where recovery was able to occur through asexual means (no border), seagrass shoot density was significantly higher than in plots which relied on sexual means (bordered) from 2.5 - 4.5 months post clearing (Figure 14 and 15; Appendix 3 and 4). At the last sampling event for Round 1 (December 2012 - 20 months after clearing), treatments that had been cleared and which were surrounded by a border (preventing asexual recolonisation) had significantly lower shoot counts than treatments that were cleared and not enclosed by a border, although above-ground biomass was the same. However, for Round 2 (13 months after clearing), the cleared, bordered treatments still had significantly less above-ground biomass and shoots than cleared, non-bordered treatments.

Above-ground biomass in treatments that could be colonised asexually (cleared, no border) recovered to the same density as undisturbed controls 12 months after clearing in Round 1 only (Figure 14; Appendix 3 and 4). In Round 2, seagrass above-ground biomass was still significantly lower after 13 months, although the upward trend of density in this treatment indicates that recovery to undisturbed levels is likely within a short period of time. In these same treatments (cleared, no border) shoot density recovered to undisturbed levels at a faster rate, by 5.5 - 6 months after clearing for both rounds (Figure 14; Appendix 3 and 4). Where recovery was dependent on sexual means (i.e. recovery from seed bank or seed recruitment; bordered), seagrass demonstrated little recovery during the first 12 - 13 months post clearing. Between 12 and 20 months post clearing seagrass above-ground biomass recovered to the same level as in corresponding control plots (Figure 14; Appendix 3 and 4).

The most dominant species in uncleared controls for the subtidal sites by shoot count was *Syringodium isoetifolium*, accouting for between 60-70% of the species composition throughout the study. Seagrass colonisation of disturbed plots in the subtidal was heavily dependent upon the pioneering *Halophila* species (*H. spinulosa* and *H. ovalis*). Recovery was likely to have occurred by both asexual (rhizome extension) and sexual (seeds and vegetative fragments) means (Figure 15).

In cleared treatments open to asexual recovery (non-bordered) *Syringodium isoetifolium* also began to recolonise plots from an early stage and displaced both *Halophila* spp*.* as densities increased (Figure 15). Densities of *Syringodium isoetifolium* remained lower than in uncleared controls until 12 - 13 months after clearing (Round 1 and 2 respectively) when the overall species composition was similar to undisturbed controls (Figure 15). At the last sample (20 and 13 months, Rounds 1 and 2 respectively), densities of *Syringodium isoetifolium, Halophila ovalis and Cymodocea serrulata* were all similar to corresponding controls. *Halophila spinulosa*, however, was still greatly elevated above control levels for Round 2 plots, despite returning to an undisturbed state by 12 months in Round 1.

Where asexual colonisation was prevented with a border, recolonisation by *Halophila spinulosa* and *Halophila ovalis* occurred from as early as one month after clearing (Figure 15). Slower growing *Syringodium isoetifolium* and *Cymodocea serrulata* were still showing little signs of recovery after 20 and 13 months (Rounds 1 and 2). *Halophila* spp*.* remained the dominant species (by shoot count) up to 20 months post clearing, accounting for 64% of the species composition as opposed to 26% in corresponding uncleared controls.

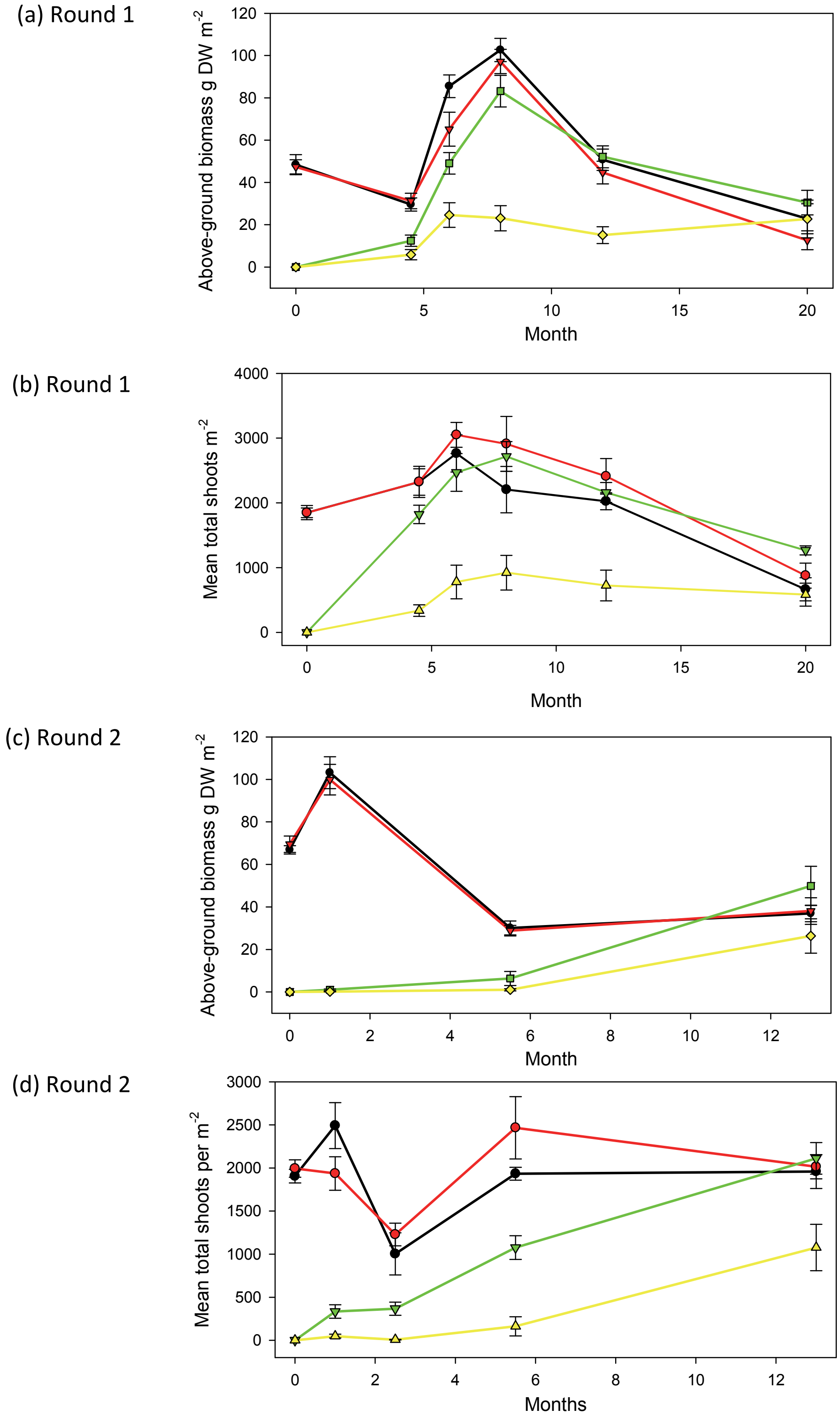


Figure 14. Mean above-ground biomass ± standard error (g DW m^{-2}) and mean total shoot density ± standard error (shoots m^{-2}) for each treatment in Round 1 (a, b) and Round 2 (c, d) in the subtidal region. Control, no border (black); control, border (red); cleared, no border (green); cleared, border (yellow).

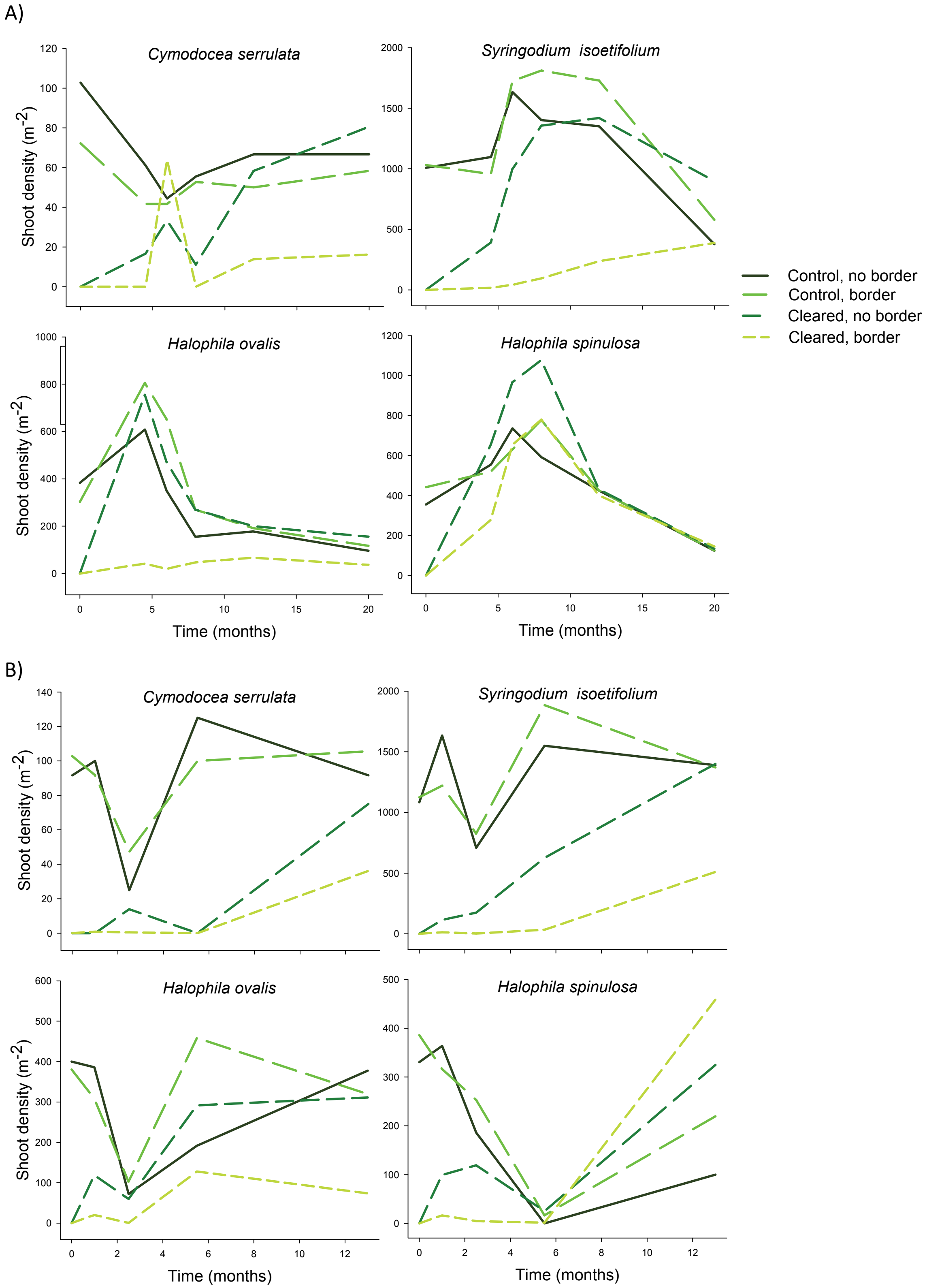


Figure 15. Mean species shoot density (shoots m^{-2}) for each treatment in the subtidal region in (a) Round 1 and (b) Round 2.

3.3.2 Seagrass reproductive assessment

The total density of seeds found at Mabuiag Island was high compared with other locations that have been assessed in north Queensland. Seeds were recorded for all eight sampling times intertidally and all three sampling times subtidally. Seed densities (all species pooled) were at their highest in autumn and winter in the intertidal and lowest in spring and summer (Figure 16). Seeds peaked in April/May each year, reaching densities of 250.3 ± 145.9 m^{-2} in April 2012. Seed densities in the subtidal were only sampled in April 2011, April 2012 and December 2012 and reached a high of 1478.8 ± 341.0 m^{-2} (Figure 17).

Although some seagrass species in both the intertidal and subtidal had significant seed banks, others did not despite their capacity to produce long-lived seeds. Seeds from five of the seven intertidal species were identified *Halodule uninervis, Cymodocea serrulata, Cymodocea rotundata, Syringodium isoetifolium* and *Halophila* spp. (Figure 16). *Halodule uninervis* seeds were the most commonly recorded each month, except in April 2011 when more than 50% of seeds were *Cymodocea serrulata.* Subtidally, seeds were dominated by *Halophila* spp. with low numbers of *Cymodocea serrulata* and *Syringodium isoteifolium* seeds identified (Figure 17).

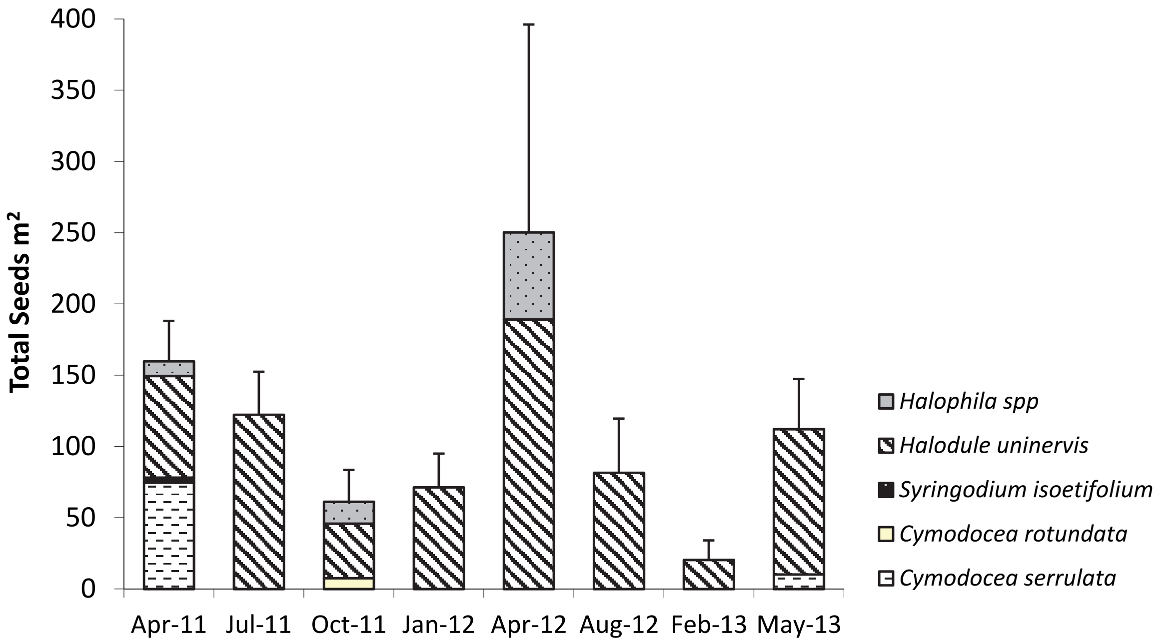


Figure 16. Mean number of seeds m^{-2} (± standard error) for each seagrass species in the intertidal region, 2011 - 2013. nb. Differentiation microscopically between seeds of *Halophila ovalis, Halophila decipiens* and *Halophila spinulosa* was not possible, therefore seeds were recorded as *Halophila* spp.

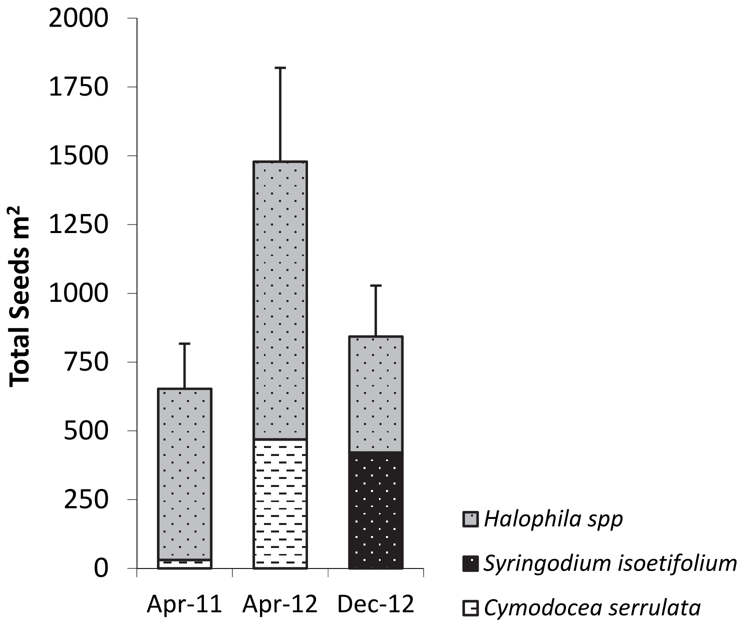


Figure 17. Mean number of seeds m^{-2} ($\pm$ standard error) for each seagrass species for the subtidal region, 2011 - 2013.

Flowering and/or fruiting was observed in both the intertidal and subtidal regions most months between April 2011 and May 2013 (Tables 4 - 7). Flowering of only two species, *Syringodium isoetifolium* (intertidal and subtidal) and *Enhalus acoroides* (intertidal only) was recorded. The density of flowering shoots in the intertidal was relatively low (maximum 16.7 ± 9.3 shoots m^{-2}) and reached much higher densities in the subtidal (maximum 232.6 ± 28.9 shoots m^{-2}). No flowering shoots were observed for any other species at the sampling times examined. Flowering was generally greatest in spring and summer and lowest in autumn and winter (Tables 4 - 7). No flowering was observed subtidally in autumn and winter (April 2011, April 2012 and August 2011).

Syringodium isoetifolium had the most extended flowering period with flowering shoots recorded in nine months of the year intertidally and four months subtidally (although not all months were sampled subtidally, see Table 4 and 5). Flowering of *Syringodium isoetifolium* only occurred in the two uncleared control treatments (bordered and unbordered) intertidally until 8.5 months post clearing (Round 1) and 13.5 months post clearing (Round 2) when low numbers (<3 shoots m^{-2}) were observed in cleared plots in which asexual regrowth was permitted. Subtidally the same pattern was observed, however flowering was first recorded in cleared plots in which asexual growth was permitted six months post clearing. No flowering was observed by *Syringodium isoetifolium* in any cleared plots in which asexual regrowth was prevented by a border. Densities of *Syringodium isoetifolium* flowering shoots were at their greatest in spring/summer in both 2011 and 2012, peaking intertidally in August 2011 (16.7 ± 9.3 shoots m^{-2}) and subtidally in December 2011 (232.6 ± 28.9 shoots m^{-2}).

Flowering shoots of *Enhalus acoroides* in the intertidal region was only quantitatively recorded in May 2011, February 2012 and June 2012, although flowers were also observed in April and May 2012 and February 2013 (Table 6). Flowering density peaked in February 2012 (2.08 ± 1.54 shoots m^{-2}) and only occurred in uncleared control treatment plots.

Fruits attached to shoots were observed in three species intertidally, *Enhalus acoroides, Thalassia hemprichii* and *Halophila ovalis*, and three subtidally, *Syringodium isoetifolium, Halophila ovalis* and *Halophila decipiens*. The density of fruiting shoots was very low both intertidally and subtidally (maximum

7.8 ± 7.8 shoots m^{-2} and 17.4 ± 12.2 shoots m^{-2} respectively). Fruiting occurred infrequently throughout the year, although densities were at their greatest in summer (Tables 4 - 7).

Table 4. Reproductive output of seagrass in the intertidal region by month at Mabuiag Island.

Species	Reproductive output	January	February	March	April	May	June	July	August	September	October	November	December
Enhalus acoroides	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Syringodium isoetifolium	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Halophila ovalis	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Halodule uninervis	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Thalassia hemprichii	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Cymodocea serrulata	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na
Cymodocea rotundata	Fruiting												
	Flowering												
	Seeds			na			na			na		na	na

Table 5. Reproductive output of seagrass in the subtidal region by month at Mabuiag Island.

Species	Reproductive output	January	February	March	April	May	June	July	August	September	October	November	December
Syringodium isoetifolium	Fruiting		na	na		na	na	na		na			
	Flowering		na	na		na	na	na		na			
	Seeds		na	na		na	na	na		na			
Halophila spp	Fruiting		na	na		na	na	na		na			
	Flowering		na	na		na	na	na		na			
	Seeds		na	na		na	na	na		na			
Cymodocea serrulata	Fruiting		na	na		na	na	na		na			
	Flowering		na	na		na	na	na		na			
	Seeds		na	na		na	na	na		na			
Cymodocea rotundata	Fruiting		na	na		na	na	na		na			
	Flowering		na	na		na	na	na		na			
	Seeds		na	na		na	na	na		na			

Table 6. Mean monthly number of fruits and flowers m^{-2} in the intertidal region from seed cores and recovery experimental plots, April 2011 – May 2013

Date	*Enhalus acoroides*		*Syringodium isoetifolium*		*Thalassia hemprichii*		*Halophila ovalis*		Total	
	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2
April 2011	0.00	0.00	0.00	1.39 ± 1.39	0.00	0.00	0.00	0.00	**0.00**	**1.39 ± 1.39**
May 2011	0.00	1.39 ± 1.39	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**1.39 ± 1.39**
June 2011	0.00	0.00	0.00	1.39 ± 1.39	0.00	0.00	1.33 ± 1.33	0.00	**1.33 ± 1.33**	**1.39 ± 1.39**
July 2011	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
August 2011	0.00	0.00	0.00	16.67 ± 11.79	0.00	0.00	0.00	0.00	**0.00**	**16.67 ± 11.79**
September 2011	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
October 2011	0.00	0.00	0.00	0.00	7.65 ± 7.65	0.00	0.00	0.00	**7.65 ± 7.65**	**0.00**
November 2011	0.00	0.00	0.00	1.38 ± 1.38	0.00	0.00	0.00	0.00	**0.00**	**5.56 ± 5.56**
December 2011	0.00	0.00	0.00	3.47 ± 2.47	0.00	0.00	0.00	0.00	**0.00**	**3.47 ± 2.47**
January 2012	0.00	0.00	0.00	1.46 ± 0.99	0.00	0.00	0.00	0.00	**0.00**	**1.46 ± 0.99**
February 2012	0.69 ± 0.69	2.08 ± 1.54	0.00	0.00	0.00	0.00	0.00	0.00	**0.69 ± 0.69**	**2.08 ± 1.54**
March 2012	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
April 2012	0*	0*	0.00	0.00	0.00	0.00	0.00	0.00	**0***	**0***
May 2012	0*	0*	0.00	0.00	0.00	0.00	0.00	0.00	**0***	**0***
June 2012	0.00	0.69 ± 0.69	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.69 ± 0.69**
July 2012	0.00	0.00	0.00	0*	0.00	0.00	0.00	0.00	**0.00**	**0***
July 2012	0.00	0.00	0.00	1.39 ± 0.97	0.00	0.00	0.00	0.00	**0.00**	**1.39 ± 0.97**
August 2012	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
September 2012	0.00	0.00	0.00	15.28 ± 8.7	0.00	0.00	0.00	0.00	**0.00**	**15.28 ± 8.7**
February 2013	0.00	0*	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0***
May 2013	0.69 ± 0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.69 ± 0.69**	**0.00**

* Seagrass flowers and/or fruits observed around experimental site, although none were recorded within plots

Table 7. Mean monthly number of fruits and flowers m^{-2} ($\pm$ 1 standard error) in the subtidal region from seed cores and recovery experimental plots, April 2011 – December 2012.

Date	*Syringodium isoetifolium*		*Halophila ovalis*		*Halophila decipiens*		Total	
	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2	Fruits m^2	Flowers m^2
April 2011	0.00	0.00	0.00	0.00	3.5 ± 3.5	0.00	**3.5 ± 3.5**	**0.00**
August 2011	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
October 2011	0.00	40.3 ± 10.6	0.17 ± 0.17	0*	0.00	0.00	**0.17 ± 0.17**	**40.3 ± 10.6**
November 2011	0.00	206.9 ± 46.2	0.00	0.00	0.00	0.00	**0.00**	**206.9 ± 46.2**
December 2011	17.4 ± 12.2	232.6 ± 28.9	0.00	0.00	0.00	0.00	**17.4 ± 12.2**	**232.6 ± 28.9**
January 2012	0.00	6.3 ± 3.9	0.00	0.00	0.00	0.00	**0.00**	**6.3 ± 3.9**
April 2012	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	**0.00**
December 2012	0.00	24.3 ± 6.9	0.00	0.00	0.00	0.00	**0.00**	**0.00**

* Seagrass flowers and/or fruits observed around experimental site, although none were recorded within plots

3.4 Discussion

Physical disturbance is a key factor in the ecology and dynamics of seagrass meadows (Hemminga and Duarte 2000; Bell et al. 1999; Fonseca and Bell 1998; den Hartog 1971). Physical disturbance has been suggested to be critical to allow the co-existence of mixed seagrass meadows (Duarte et al. 1997; Kirkman and Kuo 1990; Williams 1990), which are generally restricted to the tropical and subtropical regions (Duarte 2001). Understanding the capacity of a seagrass meadow to be resilient to physical disturbances and the impacts of disturbance on community structure requires knowledge, however, of the ability of the plants to recover from a loss via sexual or asexual means. The present study finds that there were strong differences between meadow locations (subtidal and intertidal) and species in their capacity for recovery and the mechanisms employed to recolonise from disturbances. For intertidal mixed species meadows in this study, asexual colonisation was the most important mechanism for recolonisation of cleared plots (gaps), whilst in the subtidal meadow recovery via a combination of sexual and asexual means was utilised.

Total above-ground biomass and shoot density of gaps in the intertidal site recovered asexually through rhizome extension to the undisturbed state in 5 - 8 months. Species composition in asexually recovering gaps, however, remained different to undisturbed areas through to 22.5 months after clearing and reflected the different reproductive strategies of the species present. For the subtidal sites asexual recovery of seagrasses was slower and more variable, with above-ground biomass taking at least 12 months to return to undisturbed levels. Species composition for the subtidal sites returned to be similar to the undisturbed state during the course of the study. This difference is likely a reflection of the dominance of species considered to be fast growing early colonisers in the subtidal site, compared with intertidal sites where a mix of species including larger and slower growing species such as *Enhalus accoroides*, *Cymodocea* spp. and *Thalassia hemprichii* were more common.

When recovery from surrounding seagrasses was prevented by a border (simulating large-scale seagrass loss), intertidal seagrasses were unable to recover to pre-disturbance levels during the two years of these experiments. The upward trend of seagrass biomass and shoot counts in these treatments suggested, however, that recovery was possible. Recovery to pre-disturbance species composition would likely take more time still. Subtidal seagrasses did recover to undisturbed levels during the study, although species composition also remained different. This indicates that long-term recovery from large-scale seagrass loss is likley to be dependent on settlement of rhizome or asexual propagules (seagrass fragments), the external supply of seeds, and *in situ* seed reserves.

The rate of recovery of seagrass (in terms of above-ground biomass) into experimentally created small gaps in the intertidal meadow at Mabuiag Island was relatively fast compared to similar studies in tropical seagrass communities (Table 8). Recovery times of greater than 1.4 years have been reported from the Philippines (Rollón et al. 1999). Conversely, recovery rates of seagrass in the subtidal region at Mabuiag Island were comparatively slow with one study by Unsworth et al. (2010) reporting recovery of *Halophila spinulosa* from as early as 2 months post clearing. Of these studies, only three examined recovery rates when asexual reproduction was prevented (Unsworth et al. 2010; Rasheed 2004; Rasheed 1999) and reported that recovery was not completed during the life of the studies, which was as long as 26 months in (Rasheed 2004).

Table 8. Seagrass recovery rates into experimentally cleared gaps.

Location	Species	Recovery time*	Study
Philippines (intertidal)	*E. acoroides, T. hemprichii, C. rotundata, S. isoetifolium, H. uninervis, H. ovalis*	1.4 – 5.7 years	Rollon et al. 1999
Cairns, Queensland (intertidal)	*Z. capricorni*	12 months	Rasheed 1999
Mabuiag Island (subtidal)	*S. isoetifolium, H. spinulosa, C. serrulata, H. ovalis, H. decipiens, C. rotundata*	12 months	This study
Brazil (subtidal)	*H. wrightii*	9 months	Creed et al. 1999
Green Island, Queensland (subtidal)	*H. uninervis, C. rotundata, C. serrulata, S. isoetifolium, H. ovalis, Z. capricorni*	7 months	Rasheed 2004
Mabuiag Island (intertidal)	*C. serrulata, C. rotundata, T. hemprichii, S. isoetifolium, H. uninervis, E. acoroides, H. ovalis*	5.5 - 8 months	This study
Abbot Point, Queensland (subtidal)	*H. uninervis*	4 months	Unsworth et al. 2010
Abbot Point, Queensland (subtidal)	*H. spinulosa*	2 months	Unsworth et al. 2010

* In terms of above-ground biomass. Asexual recovery not prevented

Flowering and fruiting for a number of species was rarely seen at Mabuiag Island and seeds in the sediment were also limited to a few species. Studies quantifying seagrass flowering intensity and seed bank production also demonstrate that reproductive effort varies greatly among species and sites (e.g. Inglis 2000; Inglis and Smith 1998; Cambridge and Hocking 1997; Gallegos et al. 1992). Flowering was only recorded for two species at Mabuiag Island, *Enhalus acoroides* and *Syringodium isoetifolium*, despite flowering for all Mabuiag Island seagrass species being reported in other geographic locations (McMillan 1980). *Syringodium isoetifolium* flower density was seven times greater at Mabuiag Island than at Green

Island, north Queensland (>200 flowers m^{-2} compared to <30 m^{-2})(Rasheed 2004).Densities of *Enhalus acoroides* flowers were small in comparision to *Enhalus acoroides* dominated meadows in the Philippines (2 flowers m^{-2} compared to 26 m^{-2}) (Rollón et al. 2003). Lack of flowering for all other seagrass species may be due to an absence of favourable environmental conditions for flower development. Flowering in some seagrass species is only possible during a narrow range of light (Rollón et al. 2003; McMillan 1980), temperature (Rollón et al. 2003; De Cock 1981) and salinity (McMillan 1976). Presumably some of the other species did flower during the course of the study outside of specific sampling times as fruits attached to the shoots were recorded for both *Halopila ovalis* and *Halopila decipiens*, and seeds were recorded for a number of the other species in sediment cores.

Substantial sediment seed banks have been documented in fast-growing seagrass of the genus *Halophila*, *Halodule* and *Cymodocea* (Inglis 2000; Orth et al. 2000; McMillan et al. 1982; McMillan 1981). Densities of *Halodule uninervis* can reach up to 10,000 seeds m^{-2} (Inglis 2000). Sizable subtidal seed banks for *Halophila* spp. (approx 1000m^{-2}), *Cymodocea serrulata* (approx 500m^{-2}), and *Syringodium isoetifolium* (approx 450m^{-2}) were identified intermittently at Mabuiag Island. Most likely, these *in situ* seed reserves provided the biggest source of recovery as the subtidal site regularly experienced currents in excess of 6 knots during the twice monthly spring tides. Strong currents presumably make it difficult for rhizome or seagrass fragments to take root and may explain why initial recovery by rhizome extension from existing plants was slow.

The most prolific seeds in the intertidal meadow were *Halodule uninervis* (approx 200m^{-2}). Very low densities of *Cymodocea rotundata* seeds were recorded in October 2011 only. The lack of *Enhalus acoroides* and *Thalassia hemprichii* seeds was expected as fruits and seeds of these species tend to float or remain on the surface of the sediments, limiting these species ability to develop persistent seed banks. Recovery of these species would be heavily dependent on asexual means or an external supply of seeds. Long-distance export outside *Enhalus acoroides* and *Thalassia hemprichii* meadows may be considerable as seeds have the capacity to float for days and hours, respectively (Lacap et al. 2002). *Cymodocea rotundata* has smaller seeds that are set at or within the sediment, similar to *Halodule uninervis,* which has been demonstrated to limit dispersal capacity (Inglis 2000).

Dormancy and germination traits of different species' seeds may also impact the recovery ability of seagrass through sexual reproduction in Torres Strait. Very little recovery of intertidal seagrasses was recorded in the first 18 months for plots dependent on sexual reproduction, followed by a sudden increase. This recovery was driven almost solely by *Halodule uninervis* and *Cymodocea serrulata*. This recovery may have been due to a seed germination event. Seeds of *Cymodocea, Halodule, Halophila and Syringodium* species have all been identified as having the ability to stay dormant in sediments from 12 months to 49 months (Reyes et al. 1995; McMillan 1991), awaiting ideal conditions for growth. Many studies have been conducted on what prompts germination of dormant seeds in terrestrial plants, but there is a paucity of similar studies on the physiological and environmental cues that drive dormant seagrass seeds to germinate. Environmental factors that have been linked to seagrass seed germination include salinity, temperature, light, and sediment characteristics such as oxygen levels (Orth et al. 2000; Brenchley and Probert 1998). The interactions between environmental factors that provide ideal conditions seed germination are numerous and species-specific. For example, Caye and Meinesz (1986) reported that seasonal water temperature variations appeared to control germination timing in some *Cymodocea* species, resulting in spring germination, but this was not the case for *Zostera noltii* at the same location.

Seagrasses commonly have a range of species-specific life histories and physiological adaptations enabling adaptation to different niches. Given there is a trade-off between competitive ability and colonisation potential, recently disturbed areas tend to be dominated by pioneer species, such as *Halophila* spp. and *Halodule uninervis* (Rasheed 2004; Birch and Birch 1984) that are characterised by abundant seed production, high dispersal power and rapid growth, which are eventually displaced by larger, slower-growing species that are superior competitors (Olesen et al. 2004; Tilman 1994). This pattern was evident in the subtidal region with *Halophila ovalis and Halophila spinulosa* dominating early recolonisation before being competitively displaced by *Syringodium isoetifolium*. In the intertidal meadow, *Halophila ovalis* was displaced relatively early in the recovery process and *Halodule uninervis* also showed signs of displacement as larger species recovered.

Our results indicate that most seagrass species at Mabuiag Island would be able to recover from smaller scale disturbances relatively quickly by capitalising on their highly clonal nature, providing some adult plants remain. Recovery from larger scale disturbances would be more reliant on colonisation by sexual propagules meaning recovery may take years, if it occurs at all for some species. Large-scale disturbance of seagrass meadows in this region would likely have negative implications for a range of ecologically and economically important fauna, including dugong and turtle, in the region.

4 SEAGRASS PRODUCTIVITY

4.1 Introduction

Seagrasses form some of the most productive ecosystems on earth, rivalling many terrestrial ecosystems. Seagrasses have high primary productivity and are the basis of many marine food webs (Hemminga and Duarte 2000), provide nutrients and organic carbon to the oceans, and contribute significantly to carbon sequestration (Duarte et al. 2011). Productivity can vary markedly, however, between locations and species (Rasheed et al. 2008). Seagrass meadow primary productivity is a function of seagrass species composition, daily growth rates, shoot and rhizome density and meadow size (Unsworth et al. 2010; Rasheed et al. 2008; Rasheed et al. 2006). Seasonal changes can have a strong influence on all factors and consequently on total productivity (Rasheed et al. 2008).

A study by Rasheed et al. (2008) of productivity of seagrasses at the Orman Reefs (9 km north east of Mabuiag Island) found that net primary production of the reef platform seagrasses identified was higher than that determined for a mangrove forest in north Queensland and higher than many freshwater and brackish autotrophic communities. Sources of marine autotrophic production are likely to be critically important for local dugong and turtle populations. Measuring productivity (growth) rates of seagrass meadows at Mabuiag Island provides a means to assess their potential contribution to marine primary productivity and how this may be influenced by future environmental and habitat change and including disturbances from anthropogenic impacts such as shipping accidents and climate change. Measuring meadow productivity also provides a means in which the amount of carbon being incorporated into the Mabuiag Island seagrass ecosystem can be measured.

The large intra-annual changes in seagrass abundance at Mabuiag Island are likely to have consequences for primary productivity. This is the first time that the seasonality of productivity of Torres Strait seagrasses was measured. This data provides an insight into seagrass productivity at the shoot (above-ground) and rhizome/root (below-ground) level.

The objectives of the seagrass productivity program were to:

1. Measure above-ground and below-ground seagrass productivity of Mabuiag Island seagrasses;
2. Determine any seasonal change in productivity.

4.2 Methods

The primary productivity of intertidal seagrass was measured quarterly from April 2011. Unfortunately, consistently poor weather prohibited the collection of productivity data for subtidal seagrasses and logistical issues prevented the collection of *in situ* productivity measurements for *Halophila* species found at Mabuiag Island. Values for this species collected from the nearby Orman Reefs were used (Rasheed et al. 2008). We used techniques outlined in Short and Duarte (2001) to determine the productivity of each seagrass species found within the meadows, carbon produced and meadow turnover time for Mabuiag Island seagrass meadows (Figure 18). These methods have also been applied to determine productivity of seagrass meadows at the Orman Reefs, Torres Strait (Rasheed et al. 2008) and at Abbot Point (Unsworth et al. 2010).

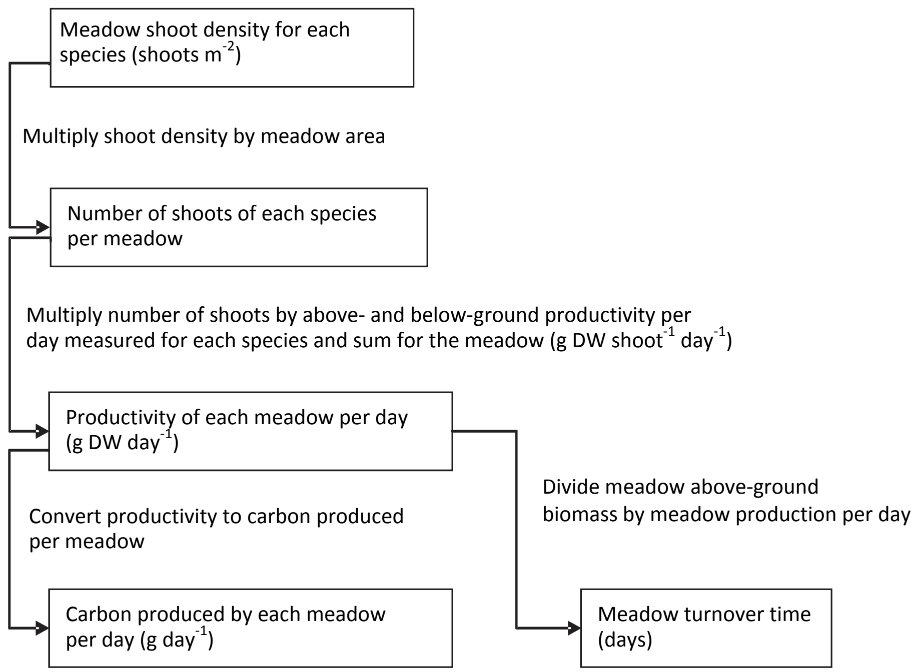


Figure 18. Flow chart detailing methods for calculating primary productivity, carbon produced, and turnover time for seagrass meadows at Mabuiag Island (adapted from Rasheed et al. 2008).

4.2.1 Meadow shoot density

Seagrass species shoot densities were collected monthly as part of the recovery experiment procedures. The mean shoot density for each species in each meadow (shoots m^{-2}) was converted to number of shoots of each species per meadow by multiplying the shoot density by the meadow area which was determined from the baseline surveys in 2009 (subtidal meadow) and 2010 (intertidal meadow).

4.2.2 Above- and below-ground production of species

Productivity information for species found in the intertidal meadow was collected using a combination of two methods according to the growth habits of the species found in the meadows:

1. *Leaf marking* - For leaf replacing seagrass species, the leaf growth rate was determined using an in situ leaf marking method. A hole was punched through all the leaves of an individual shoot using a syringe, just below the top of the basal meristem (sheath). As the leaves grow the pinhole scar from needle punching moves upwards from the basal meristem. The new leaf growth was any growth that occured between the hole in the sheath and the scar on the leaf. Plants were harvested a minimum of 12 days after marking and brought back to the laboratory for separation into old and new growth (Plate 3).
2. *Rhizome tagging* – Rhizome tagging was used to determine the leaf growth rate and the below-ground production of all species. Rhizomes were tagged at the basal meristem behind the growing tip with a coloured piece of wool (Plate 4). Subsequent growth of the tagged seagrass produced a new shoot and roots that trap the wool loop in the newly formed node. Tagged seagrasses were harvested a minimum of 12 days after tagging and biomass of new leaf material measured in the laboratory.

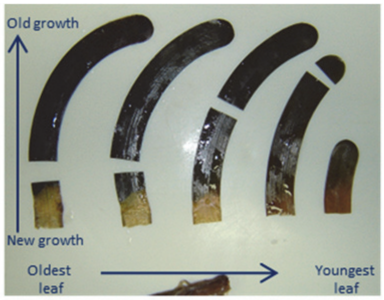


Plate 3: "New" and "old" leaf sections ready to be measured

Plate 4: *Syringodium isoetifolium* rhizome tagged with red wool to determine rhizome growth rate

In order to reduce the error associated with weighing very small and light sections of individual leaves, the samples for each species within each growth method (leaf marking or rhizome tagging) were pooled and the old and new leaf components were weighed. Dry weight per unit of leaf area was calculated by dividing the pooled weight by the surface area of leaves obtained from a CID Bio-Science Laser Leaf Area Meter or from the scanning software 'ImageJ'. 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.

4.2.3 Above-ground productivity of the intertidal meadow

To calculate the total above-ground productivity of the intertidal meadow 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 (Figure 18). It was assumed that new growth produced at the rhizome growing end would be equal to the death rate at the rhizome origin, therefore meadow productivity was based on only leaf marking techniques. Meadow above-ground productivity was expressed as dry weight added for each meadow per day (g DW day^{-1}) and was calculated for each quarter. A literature derived value was used for *Halophila ovalis* from the nearby Orman Reefs (Rasheed et al. 2008) as we were unable to obtain in situ data for this species. Where we were unable to obtain species data for every quarter we used values derived two ways:

1. Where only one quarter of data was missing and variability between results from available data was minimal, an average of the quarterly values were used; or
2. Where two quarters were missing, it was deduced that growth rates would be similar during the growing season (as determined by seasonal biomass patterns and productivity experiment results) sampling events; and during the senescing season sampling events and that these values could be applied to the missing months.

4.2.4 Meadow turnover

The turnover time of the intertidal meadow was measured by dividing the meadow biomass (g DW m^{-2}) by the meadow productivity (g DW m^{-2} day^{-1}). The number of days required for a meadow to completely turnover its current standing above-ground biomass was then calculated (Figure 18).

4.2.5 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 used by (Rasheed et al. 2008) and was based on a range of literature values (Atkinson 1983; Koike et al. 1987; Erftemeijer 1994) that were geographically and environmentally applicable.

4.2.6 Statistical analysis

All data presented in the results are shown as means (± standard error), except where otherwise stated. The species leaf production values were analysed to determine differences between each quarter. Only data collected *in situ* was analysed; data derived from other means were excluded. Analysis of variance (ANOVA) was conducted in SigmaPlot v.11.0. Where data did not conform to the assumptions of ANOVA, data were transformed. Where data continued to differ from the assumptions of ANOVA the test was still conducted, but in order to minimise the possibility of recording a Type 1 error, an α level of 0.01 was used instead of $\alpha = 0.05$ (Underwood 1997). Where a sigificant treatment difference was detected, a post-hoc LSD (equal variances) or Behrens Fisher Test (unequal variances) was permformed to determine differences amongst quarters. Detailed results are presented in Appendix 5.

4.3 Results

4.3.1 Productivity of Mabuiag Island seagrasses species

Net above-ground productivity varied markedly between species both within and between quarterly sampling events according to shoot size (Tables 9, 10; Figure 19). The structurally largest species, *Enhalus acoroides*, consistently added the greatest dry weight per shoot per day (>6.0 mg DW shoot^{-1} day^{-1}) and was an order of magnitude higher than *Cymodocea serrulata, Thalassia hemprichii* and *Cymodocea rotundata* for most sampling periods except October 2011 (Figure 19). The smallest species, *Syringodium isoetifolium* and *Halodule uninervis* added the least amount of biomass, contributing <0.7 mg DW shoot^{-1} day^{-1} (Figure 16).

A seasonal change in above-ground productivity was evident for some species at Mabuiag Island, with production at a low in autumn, increasing during winter to a peak in spring before rapidly decreasing towards the end of summer (Figure 19). New leaf growth production was significantly higher in October 2011 than in April 2011 for *Cymodocea rotundata, Cymodocea serrulata, Syringodium isoetifolium* and *Halodule uninervis* (Figure 19; Appendix 5). Only *Enhalus acoroides* showed no significant difference in production rates between quarterly sampling events. These results were surprising given that above-ground biomass was found to be at its peak in summer and lowest in winter (Figure 19). This may suggest that there is a lag time between seagrasses investment in production and a measurable change in above-ground biomass, possibly through an investment in below ground stores in the rhizomes that are depleted during peak growing times.

Investment in below-ground growth was also seasonal for seagrass at Mabuiag Island, with the fastest growth rates of rhizomes occurring in winter or spring for all species measured in 2011, and remained true for 2012 with the exception of *Cymodocea rotundata and Syringodium isoetifolium.* In July 2011, *Syringodium isoetifolium* recorded the fastest rhizome growth rate of 3.16 ± 0.65 mm day^{-1} while *Cymodocea rotundata* was the slowest at 0.85 ± 0.12 mm day^{-1} (Table 10). Shoot growth rates of species in April 2011 and January 2012 were extremely low, slowing to as little as 0.11 mm day^{-1} for *Halodule uninervis* in April 2011 (Table 9). In October 2012 rates of rhizome extension were similar to peaks in July 2011, with *Syringodium isoetifolium* again showing the fastest growth rate (4.21 ± 0.55 mm day^{-1}) while *Cymodocea rotundata* was the slowest at 1.17 mm day^{-1} (Table 10).

Table 9. Mean daily rates of new growth (cm^2 $shoot^{-1}$, $\pm$ standard error) for Mabuiag Island seagrasses, April 2011 – July 2012.

Species	Shoot growth cm^2 day^{-1}					
	Apr-11	Jul-11	Oct-11	Jan-12	May-12	Jul-12
Cymodocea rotundata	0.23 ± 0.06	0.47 ± 0.04	1.12 ± 0.16	0.47 ± 0.14	0.25 ± 0.06	0.20 ± NA
Cymodocea serrulata	0.58 ± 0.06	NA	1.1 ± 0.06	NA	NA	0.64 ± 0.05
Enhalus acoroides	1.55 ± 0.48	1.53 ± 0.33	1.48 ± NA	NA	NA	NA
Halodule uninervis	0.11 ± 0.03	0.17 ± 0.03	0.29 ± 0.02	0.11 ± NA	NA	NA
Syringodium isoetifolium	0.03 ± 0.01	NA	0.16 ± 0.01	NA	NA	NA
Thalassia hemprichii	0.66 ± 0.46	0.52 ± 0.07	1.83 ± 0.21	0.55 ± NA	0.42 ± 0.16	NA

Table 10. Mean daily rates of new rhizome growth (mm day^{-1}, $\pm$ standard error) for Mabuiag Island seagrasses April 2011 – May 2013.

Species	Rhizome growth mm day^{-1}						
	Apr-11	Jul-11	Oct-11	Jan-12	Sep/Oct -12	Feb-13	May-13
Cymodocea rotundata	2.54 ± NA	0.85 ± 0.12	2.26 ± NA	2.50 ± 0.46	1.17 ± NA	4.31 ± NA	1.16 ± 0.52
Cymodocea serrulata	0.75 ± 0.23	1.61 ± 0.42	1.42 ± 0.23	1.56 ± 0.56	1.87 ± 1.08	NA	0.84 ± 0.74
Halodule uninervis	0.17 ± NA	1.22 ± 0.24	1.45 ± 0.26	0.25 ± 0.20	1.36 ± 0.62	NA	NA
Syringodium isoetifolium	NA	3.16 ± 0.65	3.18 ± 0.61	1.37 ± 0.23	4.21 ± 0.55	NA	1.07 ± NA

* *Enhalus acoroides* and *Thalassia hemprichii* was not tagged

Cymodocea rotundata

Average daily leaf growth for *Cymodocea rotundata* differed markedly between quarters. Above-ground productivity was 0.85 ± 0.12 mg DW $shoot^{-1}$ day^{-1} at its lowest in July 2011, increased significantly to 2.50 ± 0.46 mg DW $shoot^{-1}$ day^{-1} in January 2012, and reached a peak of 4.31 mg DW $shoot^{-1}$ day^{-1} in February 2013. Productivity rates significantly fell by May 2013 (Figure 19; Appendix 5). Leaf material added per day was highest in October 2011 (1.12 ± 0.16 cm^2 day^{-1}) (Table 9).

Total growth measured from the rhizome tagging method (above- and below-ground growth of sheaths, leaves and rhizomes) of *Cymodocea rotundata* showed a slightly different pattern with production peaking at 6.50 ± NA mg DW $shoot^{-1}$ day^{-1} in February 2013 (Figure 19). Rhizome extension growth rates ranged from 0.85 ± 0.12 mm day^{-1} in July 2011 to 4.31 mm day^{-1} in February 2013 (Table 10).

Cymodocea serrulata

Average daily leaf growth for *Cymodocea serrulata* differed markedly between April 2011 (0.58 ± 0.06 cm^2 day^{-1}) and October 2011 (1.1 ± 0.06 cm^2 day^{-1}). Above-ground productivity was significantly higher in October 2011 (2.69 ± 0.15 mg DW $shoot^{-1}$ day^{-1}) than in April 2011 (1.44 ± 0.15 mg DW $shoot^{-1}$ day^{-1}).

Productivity measured for the rhizome meristems (above- and below-ground growth of sheaths, leaves and rhizomes) of *Cymodocea serrulata* showed a slightly different pattern with production peaking at 5.75 ± 0.13 mg DW shoot^{-1} day^{-1} in July 2011 (Table 9). Rhizome growth rates ranged from 0.75 ± 0.23 mm day^{-1} in April 2011 to 1.87 ± 1.08 mm day^{-1} in October 2012 (Table 10).

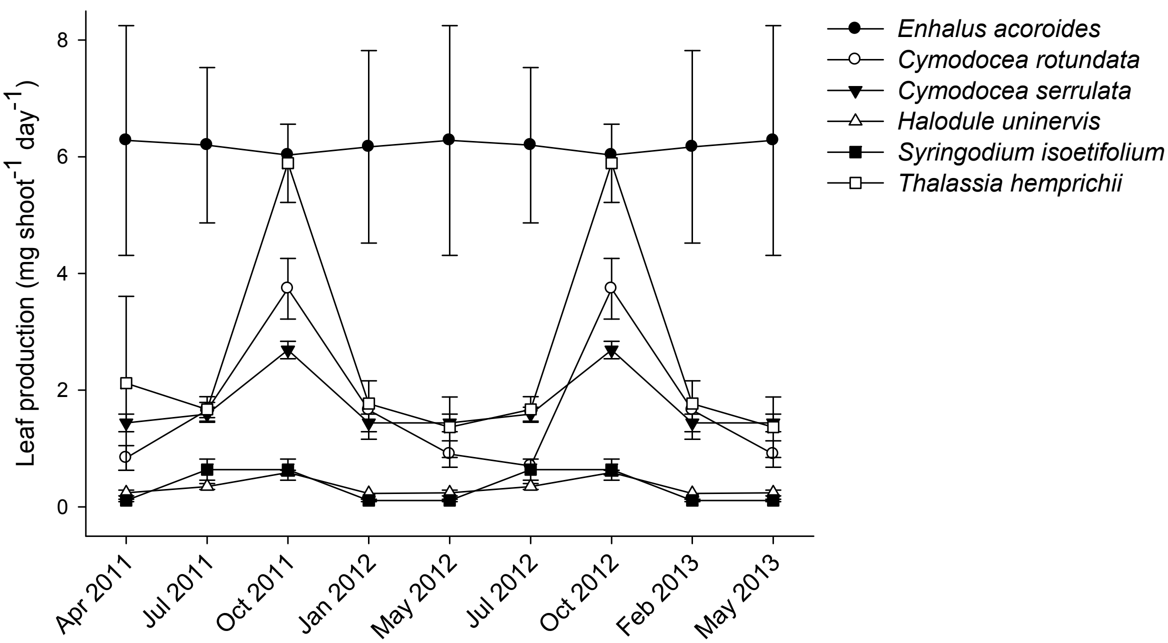


Figure 19. Mean leaf production rates (mg shoot^{-1} day^{-1} ± standard error) of Mabuiag Island seagrasses, April 2011 – May 2013.

Enhalus acoroides

Average daily leaf growth per shoot for *Enhalus acoroides* was consistent between quarters, ranging from 1.48 cm^2 day^{-1} in October 2011 to 1.55 ± 0.48 cm^2 day^{-1} in April 2011 (Table 9). Above-ground productivity had a similarly narrow range, recording 6.03 mg DW shoot^{-1} day^{-1} in October 2011 to 6.28 ± 1.97 mg DW shoot^{-1} day^{-1} in April 2011 (Figure 19; Table 9; Appendix 5).

Due to the great depth at which *Enhalus acoroides* meristems sit below the substratum surface, rhizome tagging techniques were not able to be used on this species at Mabuiag Island.

Halodule uninervis

Average daily leaf growth for *Halodule uninervis* (thin and narrow leaf morphologies) was similar between most quarters. Above-ground productivity ranged from 0.23 mg DW shoot^{-1} day^{-1} in January 2012, to 0.59 ± 0.04 mg DW shoot^{-1} day^{-1} in October 2011 (Figure 19; Table 9). There was a significant difference in productivity rates between April 2011 (0.24 ± 0.05 mg DW shoot^{-1} day^{-1}) and October 2011 (0.59 ± 0.04 mg DW shoot^{-1} day^{-1}) (Figure 19; Appendix 5). Leaf material added per day was highest in October 2011 (0.29 ± 0.02 cm^2 day^{-1}) (Table 9).

Productivity measured for the rhizome meristems (above- and below-ground growth of sheaths, leaves and rhizomes) of *Halodule uninervis* followed the same pattern with production peaking at 1.24 ± 0.22 mg DW shoot^{-1} day^{-1} in October 2011. Rhizome growth rates ranged from 0.17 mm day^{-1} in April 2011 to 1.45 ± 0.26 mm day^{-1} in October 2011 (Table 10).

Syringodium isoetifolium

Average daily leaf growth for *Syringodium isoetifolium* differed significantly between April 2011 and October 2011 (Figure 19; Appendix 5). Each shoot added an average of 0.03 ± 0.01 cm^2 day^{-1} in April 2011 and 0.16 ± 0.01 cm^2 day^{-1} in October 2011 (Table 9). Above-ground productivity was significantly higher in October 2011 (0.64 ± 0.18 mg DW $shoot^{-1}$ day^{-1}) than in April 2011 (0.11 ± 0.06 mg DW $shoot^{-1}$ day^{-1})(Figure 19; Table 9; Appendix 5).

Productivity measured for the rhizome meristems (above- and below-ground growth of sheaths, leaves and rhizomes) of *Syringodium isoetifolium* showed a slightly different pattern with production peaking at 2.52 ± 0.37 mg DW $shoot^{-1}$ day^{-1} in July 2011 (Figure 19; Table 9) and being at its lowest in May 2013 (although no data was available for April 2011). Rhizome growth rates ranged from 1.37 ± 0.23 mm day^{-1} in January 2012 to 4.21 ± 0.55 mm day^{-1} in October 2012 (Table 10).

Thalassia hemprichii

Average daily leaf growth per shoot for *Thalassia hemprichii* was consistent between quarters, ranging from 0.52 ± 0.07 cm^2 day^{-1} in July 2011 to 0.66 ± 0.46 cm^2 day^{-1} in April 2011 (Table 9). Above-ground productivity had a similarly narrow range throughout 2011 until it peaked in October 2012, recording 5.89 ± 0.67 mg DW $shoot^{-1}$ day^{-1} (Figure 19; Appendix 5).

Due to the great depth at which *Thalassia hemprichii* meristems sit below the substratum surface, rhizome tagging techniques were not able to be used on this species at Mabuiag Island.

4.3.2 Above-ground productivity of the intertidal seagrass meadow and meadow turnover

The Mabuiag Island intertidal seagrass meadow had an estimated total net above-ground productivity of 0.36 tonne dry weight per day at its lowest in May 2012 and reached 1.60 t DW day^{-1} at its peak in October 2011 (Figure 20). The time required for the intertidal seagrass meadow to turn over its above-ground biomass ranged from 12 days in October 2011 to 90.59 days in May 2012 (Figure 20). As expected, the quickest meadow turnover time corresponded with the peak in above-ground productivity seen in both October 2011 and 2012. Meadow turnover time was slowest in May 2012 corresponding to the lowest total meadow production with April 2011 and May 2013 showing similar meadow turnover rates (Figure 20).

It is estimated that the Mabuiag Island intertidal seagrass meadow incorporated from 0.14 (April 2011) to 0.55 (October 2011) tonnes of carbon per day into its above-ground biomass. The rate of production per unit area similarly peaked in October 2011 at 0.90 g C m^{-2} day^{-1} (Table 11). Using the quarterly results to calculate annual productivity resulted in a value of 164 g C m^{-2} $year^{-1}$ for 2011-2012 and 180g C m^{-2} $year^{-1}$ for 2012 -2013.

Table 11. Above-ground carbon production for the Mabuiag Island intertidal seagrass meadow.

Time	Total meadow carbon production (t meadow day^{-1})	Mean carbon production (g m^{-2} day^{-1})
Apr-11	0.14	0.23
Jul-11	0.21	0.34
Oct-11	0.55	0.90
Jan-12	0.20	0.33
May-12	0.12	0.17
Jul-12	0.25	0.41
Oct-12	0.48	0.79
Feb-13	0.24	0.40
May-13	0.18	0.30

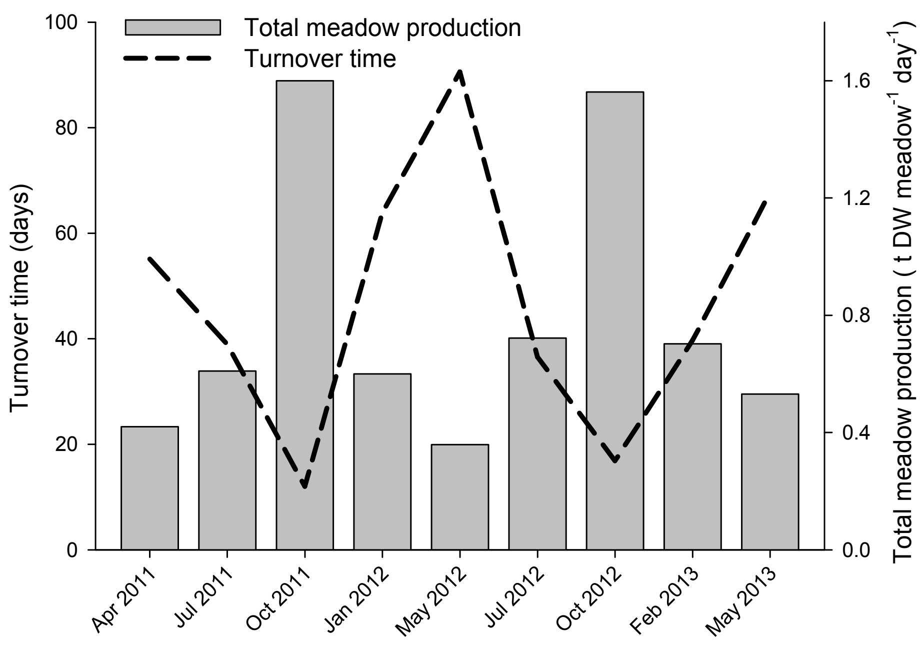


Figure 20. Total meadow above-ground production (t DW meadow day^{-1}) and meadow turnover time of Mabuiag Island intertidal seagrasses for each quarterly sample.

4.4 Discussion

Compared with other shallow aquatic environments, seagrasses are generally considered to be one of the most productive habitats (Duarte and Chiscano 1999). Productivity of Mabuiag Island seagrasses compare with other globally important ecosystems (Table 12). The net primary productivity of the Mabuiag Island intertidal meadow at its peak in October was on par with that of sub-tropical coastal seagrasses studied at Gladstone, Queensland (0.89 g C m^{-2} day^{-1}) (McCormack et al. 2013), and far above terrestrial grassland systems (0.50 g C m^{-2} day^{-1}) (Duarte and Chiscano 1999). Intertidal seagrasses at Mabuiag Island make a major contribution to local productivity that would be available for consumption by dugong and turtle.

Table 12. Net daily primary production of a range of different plant communities (g C m^{-2} day^{-1}).

Ecosystem	Location	Study	Production (g C m^{-2} day^{-1})
Grasslands	Global	(Duarte and Chiscano 1999)	0.50
Tropical Mangrove	Global	(Lugo et al. 1988)	0.92
Temperate Forest	Europe	(Luyssaert et al. 2010)	1.22
Tropical Rainforest	Amazon	(Malhi et al. 2009)	3.15
Tropical Reef Seagrass	Torres Strait	(Rasheed et al. 2008)	1.15
Seagrass Average	Global	(Duarte and Chiscano 1999)	0.94
Tropical Island Reef Seagrass	Mabuiag Island	Present study	0.90
Temperate Coastal Seagrass	New Zealand	(Turner 2007)	0.80
Sub-tropical Coastal Seagrass	Gladstone	(McCormack et al. 2013)	0.89

Above-ground productivity and carbon assimilated by Mabuiag Island intertidal seagrass meadows were strongly influenced by intra- and inter-annual changes to above-ground biomass changes, species composition and shoot density. Results of our study indicate that production was likely to be substantially higher around October than throughout the rest of the year.

The above-ground growth rates we measured for species at Mabuiag Island 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, *Enhalus acoroides* (approx. 0.006 g DW $shoot^{-1}$ day^{-1}) was double than that measured for an intertidal meadow at the nearby Orman Reefs, Torres Strait, (0.003 g DW $shoot^{-1}$ day^{-1}; Rasheed et al. 2008 (Rasheed et al. 2008) but much lower than that recorded for the species growing in similar substrates to Mabuiag Island in Philippines (0.04 to 0.07 g DW $shoot^{-1}$ day^{-1}) (Terrados et al. 1998). The above-ground productivity we measured for all other species were similar to other studies that have examined these species (Rasheed et al. 2008; Uku and Björk 2005; Udy et al. 1999; Vermaat et al. 1995a; Vermaat et al. 1995b).

The Mabuiag Island intertidal seagrass meadow was less productive than seagrass meadows of similar species composition at the nearby Orman Reefs. The mean above-ground production of the meadow from our study in April was substantially lower than values recorded by Rasheed et al. (2008) for March 2004 (0.69 g DW m^{-2} day^{-1} compared with five meadows ranging from 1.0 to 2.63 g DW m^{-2} day^{-1}). The values recorded for October at Mabuiag Island, however, were towards the high end of the range at Orman Reefs (2.11 g DW m^{-2} day^{-1}). The high productivity at Orman Reefs in March was remarkable given that the mean above-ground biomass (and presumably shoot density) of the meadows were substantially lower than for Mabuiag Island (38.01 g DW m^{-2} (April) compared with 10.39 to 26.09 g DW m^{-2}) indicating that seagrass shoots may be much more productive at Orman Reefs at that time of year, but not necessarily throughout the entire year. Alternatively, this may simply be a reflection of more favourable conditions for seagrass growth being present in 2004 than during this study in 2011-2012.

For species capable of replacing their leaves, production at the rhizome meristem (growing tip; new leaf plus rhizome growth) was generally much higher than for production in the leaf shoot. This production would likely have added significantly to the total production and carbon assimilated by Mabuiag Island 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 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 Mabuiag Island (Brouns 1987) (17% for *Thalassia hemprichii*, 34% for *Cymodocea serrulata*, 50% for *Cymodocea rotundata* and 69% for *Syringodium isoetifolium*).

The intertidal seagrass meadow at Mabuiag Island had a relatively rapid turnover time with the meadow able to replace its above-ground biomass from as little as 12 days in October. Meadow turnover time was affected seasonally, however, with turnover taking up to 90 days in May when productivity was lowest. Turnover time was a reflection of the species composition with the meadow's most dominant species (by biomass) having very long reported turnover times in literature. *Cymodocea serrulata* is typically a slow species to turnover its biomass, taking up to 37 days at the Orman Reefs (Rasheed et al. 2008), 60 days in the Philippines and up to 100 days in our study. Similarly, two further species which form dominant components of the meadow, *Cymodocea rotundata* and *Syringodium isoetifolium,* also have slow turn over times (Rasheed et al. 2008; Uku and Björk 2005; Vermaat et al. 1995b). The slow turnover for these three species was offset somewhat at Mabuiag Island due to the presence of faster turnover species within the meadows such as *Thalassia hemprichii* and *Halodule uninervis* which turned over their above-ground biomass as quickly as every 7 days.

Net carbon productivity at Mabuiag Island (ranging from 0.23 to 0.90 g C m^{-2} day^{-1}) was similar to other tropical seagrass meadows that have been studied (Rasheed et al. 2008; Moriarty et al. 1990; Kenworthy et al. 1989; Lindeboom and Sandee 1989). Measurements of mixed species seagrass meadows similar in species composition to our site in Indonesia had a net carbon production of 0.06 to 1.06 g C m^{-2} day^{-1} (Lindeboom and Sandee 1989). While production at Mabuiag Island was typical 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).

This study provides an initial assessment of the above-ground production and carbon assimilated by Mabuiag Island seagrasses. It is likely that the productivity and carbon assimilated could vary from the estimated figures due to the inter-annual changes in factors that influence seagrass growth, and because meadow size is not constant and was likely to have varied seasonally. The net primary production of seagrasses at Mabuiag Island is likely to be an important source of carbon for marine ecosystems in the 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. 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 area of intertidal seagrass at Mabuiag Island (2,190 ha; see Taylor et al. (2010) represents a substantial proportion of the available shallow seagrass habitat of the central Torres Strait.

5 GENERAL DISCUSSION

Torres Strait supports some of the largest and most diverse seagrass communities in the world. Seagrasses in the Torres Strait remain in extremely good condition and have to date been insulated from the declines noted in many other parts of the world. Seagrass meadows are being rapidly lost globally by around 5% per year, and at least a third of the global seagrass area has been lost since World War II (Waycott et al. 2009). Seagrasses of the Torres Strait region are likely to be under increasing pressure in the future from the predicted effects of climate change, as well as the increasing risks posed by substantial increases in shipping through the region. This study provides an assessment of Torres Strait seagrass resilience, capacity for recovery, and the response of seagrasses to climate that can form the basis of understanding what the implications may be of these future pressures and by extension the implications for species such as dugong and turtle that rely on them.

5.1 Effects of predicted climate change

There has been considerable debate among scientists regarding the magnitude of predicted climate change (Schneider 1990), but there is a consensus that an accelerated warming of the Earth's surface has begun and will continue (Watson et al. 1996; Kerr 1992; Schneider 1990). The impacts of increased atmospheric carbon dioxide, elevated land and sea temperatures, increasing sea level, increasing UV radiation and a host of secondary changes will alter the conditions for growth of aquatic plants (Watson et al. 1996). At Mabuiag Island the local climate factors that most impacted seagrasses were daytime tidal exposure and rainfall. It is important to note, however, that these factors may not always be the most important climate drivers in the future. Seagrasses at Mabuiag Island currently may be living in their optimal temperature and pH range which is why changes in these factors over the two year sampling period had no apparent influence on seagrass abundance. As local climate regimes change this may no longer be the case.

Projections for sea level rise in the Torres Strait indicate a rise of 0.84m by 2100 is possible (Suppiah et al. 2007). Sea level rise is expected to cause a change in the magnitude of tidal range: depending on coastal geomorphology and degree of tidal restriction already existing at a given location, expansion or lessening of tidal range may occur (De Jonge and De Jong 1992). Increased tidal range would impact seagrasses most at Mabuiag Island by increasing the amount of intertidal exposure at low tide. At the shallow edge of the meadow, seagrass stress due to exposure at low tide would be increased. Results from this study indicate that intertidal seagrasses are already being impacted by high levels of exposure, particularly during the autumn months, and therefore the result of further stress may see a loss of seagrass. It is unlikely that successful seaward movement of intertidal seagrass meadows would occur as the geomorphology of the island and surrounding channels would impede this.

There is some uncertainty in the rainfall projections for Australia, however most models point towards decreased total rainfall over the oceans but more extreme pulse rainfall events (resulting from intense storms and cyclones) with longer, dryer conditions in between (Poloczanska et al. 2007). Mabuiag Island seagrasses currently benefit from elevated rainfall levels over a period of 30 days. Investigations of relationships between seagrass biomass and rainfall levels over a shorter time frame (14 days) did not yield the same positive outcomes, despite similar high levels of rainfall being occasionally recorded. This may indicate that short, pulsed, high levels of rainfall are not as beneficial as steady high levels of rainfall over a longer period of time, and hence an increase in pulsed extreme rainfall events may be detrimental to Mabuiag Island seagrasses. It has been well documented that freshwater pulse events from flooding have been linked to mass diebacks of seagrass, such as the loss of >1000km^2 in Harvey Bay after severe storms and flooding (Campbell and McKenzie 2004).

Daytime tidal exposure and rainfall were identified as the two most important drivers of change in Mabuiag intertidal seagrasses, but it is important to note that these factors are intrinsically linked to other environmental factors, particularly water temperature and salinity (respectively). Pacific Ocean mean sea-surface temperatures are expected to rise 1.4 to 2.6°C by the end of the century (Australian Bureau of

Meteorology and CSIRO 2011). Increasing water temperature will directly affect seagrass metabolism and the maintenance of a positive carbon balance (Zimmerman et al. 1989; Bulthuis 1987; Evans et al. 1986; Marsh et al. 1986), which may result in changes in seasonal and geographic patterns of species abundance and distribution (Walker 1991; McMillan 1984). The direct effects of increased temperature will depend on the individual species thermal tolerances and their optimum temperatures for photosynthesis, respiration and growth. For intertidal seagrasses as a whole at Mabuiag Island, we found a positive relationship between water temperature and above-ground biomass, indicating that seagrasses are currently within their optimal range, even at peak summer water temperatures. Evidence suggests there is a critical temperature limit for seagrasses, however, above which it is expected there would be a decrease in productivity and distribution (Short and Neckles 1999).

Tropical seagrasses are typically living at the edge of their salinity thresholds (Koch et al. 2007; Walker 1985). Salinity is known to influence the structure and function of seagrass communities (Montague and Ley 1993), with salinity fluctuations capable of altering important plant biochemical and physiological processes, influencing plant metabolism, growth, development and reproduction (Koch et al. 2007; Touchette 2007). Salinity levels were between 28 to 40 ppt at Mabuiag Island which is within the known optimum range for seagrasses, however our results suggest that the optimal range in the Torres Strait may not be as high as 40ppt, as lower salinities during peak rainfall periods were associated with increased seagrass abundance. Fernandez-Torquemada and Sanchez-Lizaso (2005) and Marín-Guirao et al. (2011) both found that stress (decreased leaf growth and shoot survival) in the temperate seagrass species *Posidonia oceanica* was not observed until seagrass was exposed to salinity of 40 and 41ppt respectively. From our study the pathway of how high salinity may influence seagrass growth has not been established. It is possible that salinity levels near 40ppt impact upon seeds at Mabuiag Island and their ability to germinate. *Thalassia testudinum* and *Ruppia maritime* seeds were found to have a narrower salinity tolerance range than seedlings and mature plants (Kahn and Durako 2006). High salinity can also affect a number of physiological processes in the plant that could result in negative impacts on growth. Predicted reductions to ocean salinity levels (up to 0.34 ppt by 2090) as a result of climate change in the Pacific (Australian Bureau of Meteorology and CSIRO 2011) may provide a small buffer for Mabuiag Island seagrasses. Little research has been conducted as to how tropical seagrasses would react in the face of a gradual decline in salinity, with most work focusing on salinity increases caused by brine discharge in the Mediterranean (Koch et al. 2007; Short and Neckles 1999) or freshwater pulse events from flooding (Campbell and McKenzie 2004). Evidence suggests, however, that photosynthesis and respiration are often inhibited in aquatic plants exposed to extreme hypo-osmotic conditions (Touchette 2007). Diminished photosynthesis in seagrasses under hyposaline conditions have been observed in *Halophila ovalis* and *Zostera muelleri* under 25ppt, which is far below the predicted salinity levels for the Pacific under climate change scenarios (Ralph 1998b; Kerr and Strother 1985).

The implications of climate change for seagrasses in the Torres Strait are complex. Results from this study indicates that many seagrasses have a good capacity for recovery from impacts and a reasonable level of resilience, providing a local source of propagules remains viable. These attributes mean that acute and short lived impacts such as those associated with shipping accidents have a good prognosis for recovery. However chronic shifts in climate that push seagrass species beyond their tolerance limits have the potential to cause fundamental shifts in the seagrass community.

5.2 Implications for dugong and turtle management

Potential changes in distribution and structure of Torres Strait seagrass communities may have profound implications for local and regional biota, particularly dugong, turtle and economically important fisheries. The spatial distribution of quality food strongly influences the movement patterns and foraging behaviours of dugong (Sheppard et al. 2007). Seagrass areas in Torres Strait have undergone ‘diebacks’, or large-scale episodic losses and changes in distribution on temporal scales of up to decades (Williams 1994). Torres Strait Islanders widely reported such a dieback event in the mid-1970s and in the early 1980s (Williams 1994; Johannes and MacFarlane 1991). Although the reasons behind these diebacks remain unclear, local dugong mortality rates increased dramatically following these events (Marsh et al. 2004). A similar pattern of large-scale seagrass loss across the east coast of Queensland in 2011 resulted in an 215% and 176% increase in dugong and turtle deaths respectively (compared to 2010) primarily as a result of starvation (DERM 2011). These statistics are alarming in the face of predicted climate change scenarios and the potential negative effect on seagrasses.

While there is little to be done locally in the Torres Strait to prevent global climate-related change, the management of seagrass resources should be focused on reducing any anthropogenic impacts and risks to ensure resilience levels of local seagrass populations remain high. Repeated pulse impact events on the east coast of Queensland have resulted in reduced resilience of seagrass in some areas and reduced recovery capacity following losses, despite general climate conditions being favourable for growth (i.e. Mourilyan Harbour; Reason et al. (2012)). At present, the seagrass species most favoured as food for dugong in the Torres Strait, *Halodule uninervis* and *Halophila ovalis*, have high levels of resilience with dense seed banks established and their ability to rapidly re-colonise disturbed areas through both sexual and asexual means. Many other species found in the Torres Strait that form more minor components of the diet of dugongs and turtles have moderate levels of resilience as they rely more heavily on asexual reproduction and have the potential to take in excess of a year to recover from large-scale loss.

This research program is ongoing with continued assessment of seagrass changes against water quality and climate parameters in the coming years likely to further strengthen and resolve some of the key relationships that we have begun to establish. This will place us in a better position to examine potential implications of climate shifts to seagrass communities as well as to dugong and turtle feeding opportunities.

5.3 Recommendations

Continuation of the monitoring and research program at Mabuiag Island will provide much-needed information on how natural climate variability, and future scenarios of climate change, may impact seagrass meadows and therefore dugong and turtle feeding opportunities. These relationships require data to be collected over several seasons and years. We recommend:

1. Continue monitoring intertidal and subtidal seagrass meadows and climate variables to further assess the relationship between seagrass biomass with water quality and climate. A long term data set will allow for more accurate estimates of the strength of these relationships and provide the ability to predict how seagrasses may respond to climatic variation.

2. New experimental research should focus on how seagrasses in Torres Strait respond to some of the predicted effects of climate change, and may include the effect of increased water temperature and exposure of intertidal seagrasses.

3. Information that is collected can be incorporated into modelling the consequences of climate change on Torres Strait seagrass distribution to develop appropriate dugong and turtle management strategies that respond to potential shifts in seagrass distribution and communities.

4. Information collected in the program form part of considerations for future dugong and turtle management plans in the Torres Strait.

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A APPENDICES

A.1 Statistical Analysis

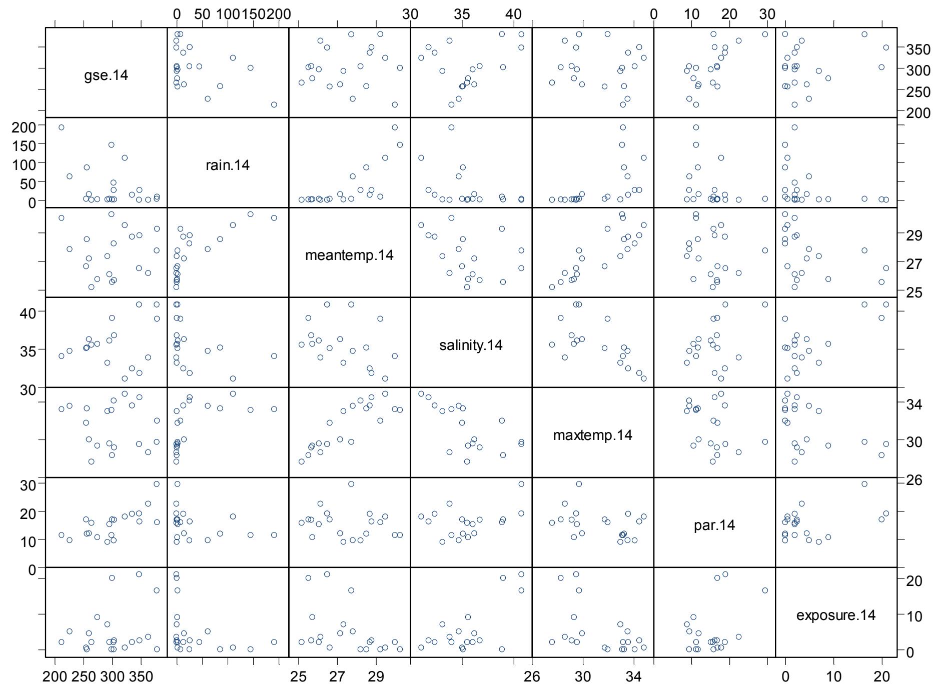

Figure 1. Scatterplot matrix of correlations between environmental variables 14 days prior to seagrass sampling in the intertidal meadow.

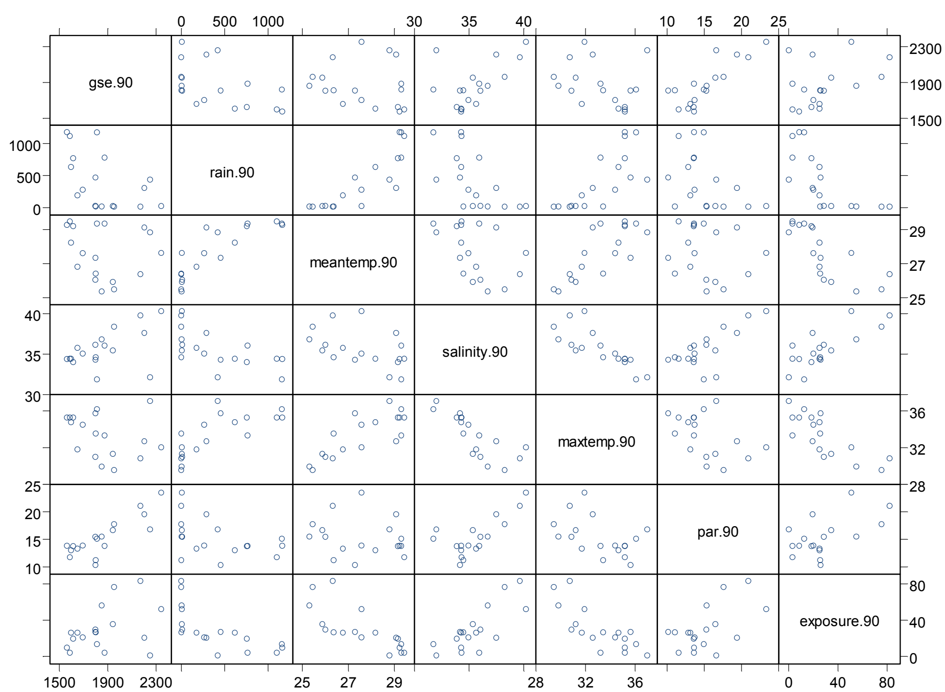

Figure 2. Scatterplot matrix of correlations between environmental variables 90 days prior to seagrass sampling in the intertidal meadow.

A.2 Statistical Analysis

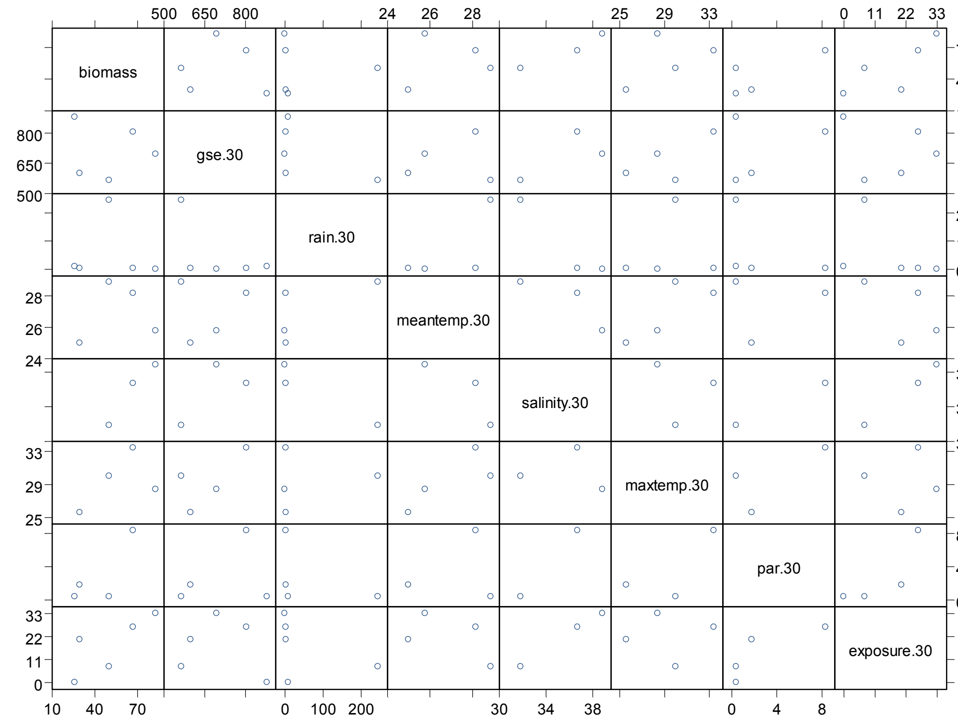

Figure 1. Scatterplot matrix of correlations between biomass and environmental variables 30 days prior to seagrass sampling in the subtidal meadow.

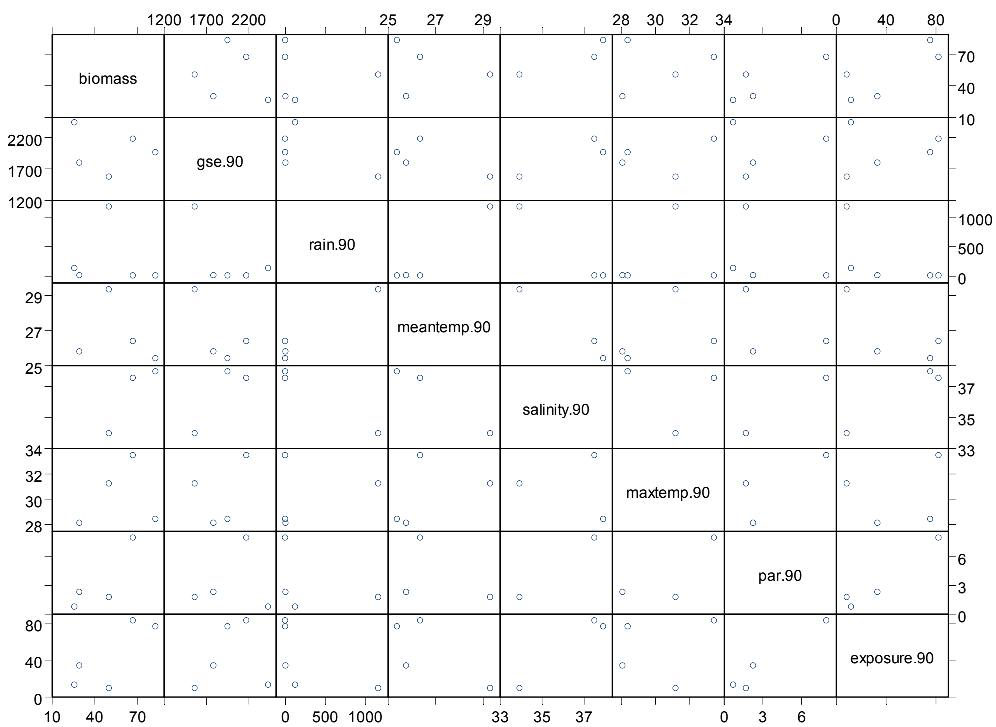

Figure 2. Scatterplot matrix of correlations between biomass and environmental variables 90 days prior to seagrass sampling in the subtidal meadow.

Results of nested two-way ANOVA tests for “Round 1” mean above-ground biomass versus treatment for each block and time (months since clearing), Mabuiag Island.

Source of variation	Time 0			Time 1			Time 2			Time 3			Time 4 & 4.5 (Subtidal)		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	1058.92	0.1770	2	142.95	0.3240	2	34.76	0.0890	2	107.17	0.4480	2	304.15	0.0750
Treatment	3	5411.79	**<0.001**	3	2818.33	**<0.001**	3	2090.90	**<0.001**	3	1725.8	**<0.001**	3	2932.01	**<0.001**
Block x Treatment	6	452.13	0.5820	6	64.66	0.7760	6	28.60	0.0780	6	59.73	0.8290	6	305.83	**0.0280**
Residual	24	567.64		24	120.86		24	12.97		24	128.97		24	105.29	
Total	35	991.12		35	343.7		35	195.00		35	252.73		35	393.32	
Subtidal	**DF**	**MS**	**P**										**DF**	**MS**	**P**
Block	2	164.014	0.1000										2	43.6	0.5910
Treatment	3	6606.53	**<0.001**										3	1425.26	**<0.001**
Block x Treatment	6	92.62	0.2430										6	93.82	0.3620
Residual	24	64.57											24	81.17	
Total	35	635.8											35	196.4	

Source of variation	Time 5.5			Time 6.5			Time 7.5			Time 8.5 & 8 (Subtidal)			Time 10		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	335.11	0.0940	2	227.51	0.3600	2	20.723	0.5960	2	28.518	0.8150	2	942.818	0.0920
Treatment	3	2827.37	**<0.001**	3	1962.11	**<0.001**	3	3570.92	**<0.001**	3	3935.21	**<0.001**	3	6493.08	**<0.001**
Block x Treatment	6	159.77	0.3200	6	194.034	0.5050	6	111.42	**0.0310**	6	140.797	0.4390	6	223.894	0.7060
Residual	24	128.43		24	213.441		24	39.229		24	138.612		24	356.629	
Total	35	376.95		35	360.803		35	353.264		35	458.118		35	893.352	
Subtidal				**DF**	**MS**	**P**				**DF**	**MS**	**P**			
Block				2	1494.76	**0.0150**				2	1716.88	**0.0020**			
Treatment				3	5969.06	**<0.001**				3	12021.9	**<0.001**			
Block x Treatment				6	160.116	0.7730				6	423.149	0.1120			
Residual				24	296.704					24	215.721				
Total				35	827.951					35	1349.03				

Source of variation	Time 11			Time 12			Time 13			Time 14			Time 15		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	1591.17	**0.0430**	2	500.554	0.0580	2	369.983	0.1080	2	42.811	0.5410	2	56.329	0.6120
Treatment	3	3316.19	**0.0010**	3	3861.08	**<0.001**	3	2952.7	**<0.001**	3	1489.35	**<0.001**	3	1968.41	**<0.001**
Block x Treatment	6	801.795	0.1380	6	201.346	0.2970	6	113.069	0.6160	6	76.628	0.3770	6	80.53	0.6400
Residual	24	441.151		24	155.497		24	150.97		24	68.001		24	112.402	
Total	35	815.125		35	500.696		35	397.136		35	189.871		35	262.821	
Subtidal				**DF**	**MS**	**P**									
Block				2	759.282	**0.0290**									
Treatment				3	2711.74	**<0.001**									
Block x Treatment				6	178.384	0.4690									
Residual				24	184.585										
Total				35	432.975										

Source of variation	Time 15.75			Time 16.5			Time 17.5			Time 18.5			Time 20		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	90.744	0.5680	2	283.37	0.3710	2	345.921	0.1240	2	56.827	0.4660			
Treatment	3	2151.90	**<0.001**	3	3585.55	**<0.001**	3	2044.44	**<0.001**	3	2041.25	**<0.001**			
Block x Treatment	6	114.661	0.6280	6	284.68	0.4250	6	269.18	0.1480	6	76.394	0.4130			
Residual	24	156.494		24	273.85		24	151.979		24	72.109				
Total	35	11081.0		35	560.11		35	345.364		35	240.753				
Subtidal													**DF**	**MS**	**P**
Block													2	1551.52	**0.0100**
Treatment													3	413.374	0.2330
Block x Treatment													6	166.872	0.712
Residual													24	268.931	
Total													35	393.218	

Source of variation	Time 22.5			Time 25.5		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	229.621	0.2340	2	261.023	0.2730
Treatment	3	949.081	**0.0020**	3	763.207	**0.0190**
Block x Treatment	6	480.831	**0.0180**	6	579.53	**0.0230**
Residual	24	148.502		24	190.169	
Total	35	278.729		35	310.083	

Results of nested two-way ANOVA tests for "Round 1" mean shoot count versus treatment for each block and time (months since clearing), Mabuiag Island.

Source of variation	Time 0			Time 1			Time 2			Time 3			Time 4 & 4.5 (Subtidal)		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	176318.11	**0.03**	2	1171697.5	0.131	2	257113	**0.028**	2	9249.361	0.836	2	668123.58	**0.005**
Treatment	3	3861555.2	**<0.001**	3	5725226.3	**<0.001**	3	1879913.9	**<0.001**	3	1403396.5	**<0.001**	3	2754376	**<0.001**
Block x Treatment	6	96254.244	0.076	6	300504.12	0.752	6	113018.56	0.134	6	9078.991	0.981	6	238971.73	0.06
Residual	23	43115.942		24	529567.9		24	61507.083		24	51424.194		24	100145.39	
Total	34	401740.55		35	972335.1		35	237378.54		35	157638.37		35	383905.57	
Subtidal	**DF**	**MS**	**P**										**DF**	**MS**	**P**
Block	2	85277.778	0.122										2	2650090.1	**<0.001**
Treatment	3	10252101	**<0.001**										3	7947808.6	**<0.001**
Block x Treatment	6	33194.444	0.513										6	315716.96	**0.009**
Residual	24	37013.889											24	83544.972	
Total	35	914695.93											35	944085.35	

Source of variation	Time 5.5			Time 6.5 & 6 (Subtidal)			Time 7.5			Time 8.5 & 8 (Subtidal)			Time 10		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	1816856.8	**0.012**	2	817727.08	**0.014**	2	701406.25	**0.004**	2	390954.86	0.073	2	1040720.8	**0.008**
Treatment	3	5743476.8	**<0.001**	3	3226324.8	**<0.001**	3	2102060.2	**<0.001**	3	3635850.7	**<0.001**	3	1329412.1	**0.001**
Block x Treatment	6	542997.1	0.184	6	375731.71	0.061	6	101383.1	0.435	6	128940.97	0.468	6	248858.74	0.252
Residual	21	329812.84		24	158343.75		24	99201.389		24	133368.06		24	176590.42	
Total	32	948499.9		35	496259.11		35	305660.71		35	447541.17		35	337171.44	
Subtidal				**DF**	**MS**	**P**				**DF**	**MS**	**P**			
Block				2	5768489.2	**<0.001**				2	6211119.7	**<0.001**			
Treatment				3	9350277.9	**<0.001**				3	7212096.5	**<0.001**			
Block x Treatment				6	178399.38	0.717				6	1355613.2	0.022			
Residual				24	290701.69					24	438842.61				
Total				35	1361001.4					35	1506412.3				

Source of variation	Time 11			Time 12			Time 13			Time 14			Time 15		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	1052277.8	**0.014**	2	260892.53	0.266	2	228064.75	0.426	2	45461.194	0.591	2	40915.444	0.926
Treatment	3	1363185.1	**0.002**	3	1162589.4	**0.003**	3	1360829.7	**0.006**	3	857289.82	**<0.001**	3	616997.66	0.344
Block x Treatment	6	298954.6	0.231	6	78429.565	0.858	6	146226.79	0.752	6	44223.231	0.785	6	322639.52	0.721
Residual	24	203406.53		24	186276.11		24	257824.53		24	84545.139		24	530153.94	
Total	35	367702.71		35	255735.92		35	331536.23		35	141634.7		35	474067.3	
Subtidal				**DF**	**MS**	**P**									
Block				2	1421892.4	**0.026**									
Treatment				3	5119120.4	**<0.001**									
Block x Treatment				6	252540.51	0.611									
Residual				24	334062.5										
Total				35	792396.83										

Source of variation	Time 15.75			Time 16.5			Time 17.5			Time 18.5			Time 20		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	313860.58	0.6620	2	2673582.5	**<0.001**	2	470914.11	0.4190	2	413208.86	0.2750			
Treatment	3	579426	0.5200	3	168728.69	0.5980	3	1459316.6	0.0620	3	893326.92	0.0530			
Block x Treatment	6	181196.69	0.9580	6	85696.75	0.9180	6	260109.48	0.8030	6	205842.19	0.6670			
Residual	24	748211.61		24	264850.14		24	521636.39		24	302805.39				
Total	35	611721.66		35	363541		35	554277.38		35	343108.03				
Subtidal													**DF**	**MS**	**P**
Block													2	930986.78	**0.0240**
Treatment													3	836826.59	**0.0210**
Block x Treatment													6	101185.7	0.821
Residual													24	213561.56	
Total													35	288715.57	

Source of variation	Time 22.5			Time 25.5		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	823345.19	0.0540	2	56996.528	0.7850
Treatment	3	165383.59	0.5840	3	133211.81	0.6390
Block x Treatment	6	229665.57	0.4990	6	114913.19	0.8070
Residual	24	250038.47		24	233229.17	
Total	35	272050.23		35	194303.08	

Results of Least Significant Difference (LSD) pair-wise comparisons of "Round 1" mean above-ground biomass versus treatment by month for intertidal and subtidal experimental blocks, Mabuiag Island March 2011 – May 2013. Means that share a common letter for each meadow are not significantly different.

Intertidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	38.01 a	46.15 a	0.0 b	0.0 b
1	30.61 a	35.84 a	4.41 b	1.34 b
2	27.85 a	31.19 a	7.55 b	0.0 c
3	27.31 a	28.23 a	7.62 b	0.91 b
4	39.04 a	37.44 a	19.21 b	0.6 c
5.5	41.38 a	37.97 a	32.15 a	2.55 b
6.5	31.77 a	25.76 a	35.59 a	2.64 b
7.5	41.53 a	40.22 a	43.81 a	2.13 b
8.5	46.21 a	40.37 a	46.21 a	2.8 b
10	62.9 a	56.94 a	70.08 a	10.67 b
11	51.98 a	46.02 a	55.1 a	13.39 b
12	53.81 a	41.18 b	49.38 ab	8.04c
13	48.62 a	38.26 a	45.12 a	8.81 b
14	38.51 a	33.11 a	37.58 a	11.11 b
15	44.1 a	34.98 a	38.6 a	10.61 b
15.75	43.69 a	36.39 a	42.42 a	10.57 b
16.5	55.55 a	39.45 a	51.3 a	11.24 b
17.5	47.67 a	42.29 a	45.28 a	15.26 b
18.5	43.64 a	37.95 a	43.64 a	12.1 b
22.5	46.12 a	44.83 a	49.02 a	26.44 b
25.5	59.64 a	55.0 a	63.78 a	42.44 b

Subtidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	48.38 a	45.38 a	0.0 b	0.0 b
4.5	29.58 a	31.21 a	12.42 b	5.84 b
6	85.51 a	65.16 b	49.05 b	24.59 c
8	102.64 a	97.18 a	83.18 b	23.1 c
12	50.73 a	44.67 a	52.13 a	15.07 b
20	20.79 a	11.61* a	30.47 a	22.75 a

* Results from n=7 due to missing data

Results of Least Significant Difference (LSD) pair-wise comparisons of "Round 1" mean shoot counts versus treatment by month for intertidal and subtidal experimental blocks, Mabuiag Island March 2011 – May 2013. Means that share a common letter for each meadow are not significantly different.

Intertidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	1030.6 a	1258.3 b	0.0 c	0.0 c
1	1696.3 a	1407.4 a	444.4 b	0.0 b
2	961.1 a	877.8 a	331.1 b	0.0 c
3	894.4 a	800 a	480.6 b	19.1 c
4	1263.9 a	1086.1 b	688.9 c	16.4 d
5.5	1518.2 a	1656.9 a	2091.7 a	191.7 b
6.5	1408.3 a	1266.7 a	1444.4 a	185.6 b
7.5	1188.9 a	1177.8 a	1291.7 a	258.3 b
8.5	1502.8 a	1405.6 a	1711.1 a	294.4 b
10	1202.8 a	980.6 a	1244.4 a	409.7 b
11	1072.2 a	1225 a	1308.3 a	448.4 a
12	1216.7 a	930.6 a	1238.9 a	467 b
13	1377.8 a	1119.4 a	1413.9 a	571.6 b
14	905.6 a	841.7 a	983.3 a	303.9 b
15	1491.7 a	1297.2 a	1544.4 a	965.9 a
15.75	1544.4 a	1366.7 a	1536.1 a	1002.1 a
16.5	1377.8 a	1111.1 a	1147.6 a	1073.4 a
17.5	1525.0 a	1425.0 a	1913.9 a	935.2 a
18.5	1447.2 a	1247.2 a	1463.9 a	787.6 a
22.5	1330.6 a	1133.3 a	1125.0 a	1002.9 a
25.5	925.0 a	975.0 a	1191.7 a	955.6 a

Subtidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	1850 a	1847.2 a	0.0 b	0.0 b
4.5	2322.2 a	2325 a	1822.2 b	337.4 c
6	2763.8 a	3050 ab	2469.4 a	778.4 c
8	2205.6 a	2911.1 b	2716.7 ab	922.6 c
12	2025 a	2411.1 a	2161.1 a	725 b
20	665.0 a	877.8 abc	1266.7 b	584.8 c

A.4 Statistical Analysis

Results of nested two-way ANOVA tests for "Round 2" mean above-ground biomass versus treatment for each block and month, intertidal experimental blocks (August 2011 – May 2013) and subtidal experimental blocks (November 2011 – December 2012), Mabuiag Island.

Source of variation	Time 0			Time 1.5 & 1.0 (Subtidal)			Time 2.5			Time 3.5			Time 5		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	82.561	**0.0410**	2	94.085	0.4350	2	135.35	0.2240	2	243.854	0.2520	2	65.34	0.6220
Treatment	3	2950.805	**<0.001**	3	1221.755	**<0.001**	3	3088.21	**<0.001**	3	5497.331	**<0.001**	3	7647.228	**<0.001**
Block x Treatment	6	56.004	0.0520	6	54.121	0.8050	6	125.99	0.2260	6	133.498	0.5790	6	64.527	0.8180
Residual	24	22.623		24	109.245		24	84.98		24	166.711		24	134.867	
Total	35	282.757		35	194.287		35	352.31		35	622.336		35	762.753	
Subtidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**						*	**DF**	**MS**	**P**
Block	2	39.94	0.4480	2	934.595	**0.0110**						Between Treatment	3	683.129	**<0.001**
Treatment	3	13963.38	**<0.001**	3	30607.52	**<0.001**									
Block x Treatment	6	19.625	0.8670	6	313.737	0.1310						Within Treatment	8	20.929	
Residual	24	48.154		24	169.195										
Total	35	1235.528		35	2846.71							Total	11		

Source of variation	Time 6			Time 7			Time 8			Time 9			Time 10		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	149.742	0.6860	2	1551.31	**<0.001**	2	664.203	**0.0130**	2	12.306	0.7110	2	196.276	0.3330
Treatment	3	5211.848	**<0.001**	3	6373.683	**<0.001**	3	2851.407	**<0.001**	3	1101.324	**<0.001**	3	1770.487	**<0.001**
Block x Treatment	6	150.261	0.8820	6	247.995	**0.0360**	6	187.702	0.2250	6	14.983	0.8580	6	56.855	0.9120
Residual	24	391.138		24	90.403		24	126.291		24	35.617		24	170.43	
Total	35	749.254		35	739.466		35	401.138		35	122.094		35	289.585	
Subtidal															
Block															
Treatment															
Block x Treatment															
Residual															
Total															

Source of variation	Time 10.75			Time 11.5			Time 12.5			Time 13.5 &13.0 (Subtidal)			Time 18		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	183.607	0.2180	2	97.125	0.5530	2	193.852	0.2420	2	294.883	0.1710	2	2169.673	**0.0150**
Treatment	3	1775.124	**<0.001**	3	3831.297	**<0.001**	3	2196.056	**<0.001**	3	877	**0.0050**	3	2749.979	**0.0030**
Block x Treatment	6	42.831	0.8850	6	526.925	**0.0170**	6	109.371	0.5440	6	146.585	0.4810	6	496.06	0.3660
Residual	24	113.176		24	159.933		24	128.549		23	154.583		24	432.405	
Total	35	247.594		35	533.946		35	306.208		34	225.844		35	750.561	
Subtidal										**DF**	**MS**	**P**			
Block										2	5676.571	**<0.001**			
Treatment										3	837.88	**<0.001**			
Block x Treatment										6	249.209	**0.0190**			
Residual										24	77.962				
Total										35	492.375				

Source of variation	Time 21		
Intertidal	**DF**	**MS**	**P**
Block	2	45.455	0.8680
Treatment	3	1650.276	**0.0070**
Block x Treatment	6	566.057	0.1480
Residual	24	319.428	
Total	35	460.71	

* Only 1 of 3 subtidal blocks surveyed. One-way ANOVA conducted.

Results of nested two-way ANOVA tests for “Round 2” mean shoot counts versus treatment for each block and month, intertidal experimental blocks (August 2011 – May 2013) and subtidal experimental blocks (November 2011 – December 2012), Mabuiag Island.

Source of variation	**Time 0**			**Time 1.5 & 1.0 (Subtidal)**			**Time 2.5**			**Time 3.5**			**Time 5**		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	481458.3	**0.003**	2	396304.5	**0.012**	2	191494.4	0.193	2	708463	**0.01**	2	195388.1	0.253
Treatment	3	9314925	**<0.001**	3	9297672	**<0.001**	3	5407492	**<0.001**	3	4939167	**<0.001**	3	3511318	**<0.001**
Block x Treatment	6	203588	**0.022**	6	287339.7	**0.008**	6	205540.7	0.124	6	125363	0.448	6	93081.6	0.657
Residual	24	66250		24	74710.42		24	108775.9		24	125449.1		24	134087.8	
Total	35	906263.4		35	920077.5		35	584266.6		35	571353.8		35	420038	
Subtidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**			*	**DF**	**MS**	**P**
Block	2	13489.58	0.748	2	811216.8	**0.016**	2	567390.3	**0.007**			Between Treatment	3	3059318	**<0.001**
Treatment	3	11419352	**<0.001**	3	12858817	**<0.001**	3	2857104	**<0.001**						
Block x Treatment	6	9924.769	0.968	6	467515.4	**0.03**	6	437838.4	**0.003**			Within Treatment	8	126087	
Residual	24	45850.69		24	163306.6		24	92729.67							
Total	35	1012714		35	1340667		35	415961				Total	11		

Source of variation	**Time 6**			**Time7**			**Time 8**			**Time 9**			**Time 10**		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	502080.3	0.063	2	120408.7	0.394	3	736986.8	**0.012**	2	44034.11	0.716	2	1068249	**0.004**
Treatment	3	3732660	**<0.001**	3	2382240	**<0.001**	3	5747370	**<0.001**	3	1603947	**<0.001**	3	2210039	**<0.001**
Block x Treatment	6	222543.2	0.263	6	166464.3	0.279	9	355078.9	0.065	6	87781.33	0.67	6	487098.6	**0.018**
Residual	24	161340		24	124341.9		32	172482.7		24	129787.3		24	151465.9	
Total	35	497416		35	324872.2		47	599324		35	244042.6		35	437839.6	
Subtidal															
Block															
Treatment															
Block x Treatment															
Residual															
Total															

Source of variation	Time 10.75			Time 11.5			Time 12.5			Time 13.5 &13.0 (Subtidal)			Time 18		
Intertidal	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**	**DF**	**MS**	**P**
Block	2	1991784	**0.0260**	2	2673583	**<0.001**	2	434911.4	0.3290	2	2711404	**0.0020**	2	11859305	**<0.001**
Treatment	3	2232972	**0.0100**	3	168728.7	0.5980	3	1630646	**0.0140**	3	742831.2	0.1000	3	147983	0.7180
Block x Treatment	6	436323	0.4900	6	85696.75	0.9180	6	1242794	**0.0160**	6	779384	**0.0550**	6	685148.3	0.0910
Residual	24	468174.8		24	264850.1		24	373094		24	318552		24	326620	
Total	35	701046.3		35	363541		35	633508		35	570653		35	1031781	
Subtidal										**DF**	**MS**	**P**			
Block										2	730777.8	0.0570			
Treatment										3	2069831	**<0.001**			
Block x Treatment										6	820957.4	**0.0100**			
Residual										24	225692.8				
Total										35	514669.1				

Source of variation	Time 21		
Intertidal	**DF**	**MS**	**P**
Block	2	106329.7	0.5630
Treatment	3	348884.2	0.1510
Block x Treatment	6	472150.6	**0.0430**
Residual	24	180664.1	
Total	35	230956.3	

Results of Least Significant Difference (LSD) pair-wise comparisons of "Round 2" mean above-ground biomass versus treatment by month for intertidal experimental blocks (August 2011 – May 2013) and subtidal experimental blocks (November 2011 – December 2012), Mabuiag Island. Means that share a common letter for each meadow are not significantly different.

Intertidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	30.54 a	32.15 a	0.0 b	0.0 b
1.5	26.1 a	22.97 a	7.73 b	2.03 b
2.5	34.93 a	38.11 a	6.35 b	2.89 b
3.5	47.4 a	51.74 a	15.55 b	0.79 c
5	64.89 a	71.15 a	42.8 b	6.63 c
6	52.63 a	52.7 a	25.27 b	2.93 c
7	53.25 a	63.44 a	38.0 b	1.97 c
8	41.67 a	48.95 ab	35.98 a	8.22 c
9	30.69 a	34.04 ab	26.77 a	9.19 c
10	33.44 a	37.43 ab	21.8 a	6.17 c
10.75	33.4 ab	36.98 a	23.09 b	5.66 c
11.5	41.58 ab	49.63 a	29.43 b	2.44 c
12.5	50.66 a	49.17 a	41.24 a	16.9 b
13.5	36.76 a	38.1 a	26.96 ab	16.83 b
18	56.5 a	60.09 a	52.4 a	19.9 b
21	56.2 ab	63.53 a	40.7 bc	33.2 c

Subtidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	66.86 a	69.53 a	0.0 b	0.0 b
1	103.18 a	99.91 a	1.0 b	0.13 b
2.5*	NA	NA	NA	NA
5.5^	30.11 a	28.87 a	6.32 b	0.97 b
13	36.91 a	38.1 a	49.92 b	26.33 c

* Shoot counts only

^ Only 1 of 3 blocks surveyed

Results of Least Significant Difference (LSD) pair-wise comparisons of "Round 2" mean shoot counts biomass versus treatment by month for intertidal experimental blocks (August 2011 – May 2013) and subtidal experimental blocks (November 2011 – December 2012), Mabuiag Island. Means that share a common letter for each meadow are not significantly different.

Intertidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	1872.2 a	1636.1 a	0.0 b	0.0 b
1.5	1955.6 a	1952.8 a	408.3 b	21.8 c
2.5	1725 a	1480.6 a	602.8 b	55.1 c
3.5	1744.4 a	1561.1 a	1127.8 b	89.3 c
5	1594.4 a	1422.2 a	975 b	195.7 c
6	1713.9 a	1308.3 b	1136.1 b	192.7 c
7	1555.6 a	1150 b	1216.7 ab	341.7 c
8	1941.7 a	1745.8 b	1402.1 b	386.3 c
9	1280.6 a	1041.7 a	1150 a	336 b
10	1472.2 a	797.2 b	1133.3 ab	310.6 c
10.75	1913.9 a	1925.1 a	1908.3 a	919.7 b
11.5	1377.8 a	1111.1 a	1147.6 a	1073.4 a
12.5	2047.2 a	1811.1 a	2088.9 a	1167.0 b
13.5	1594.4 ab	1530.6 ab	1700.0 a	1051.1 b
18	802.8 a	1066.7 a	1080.6 a	962.3 a
21	1166.7 a	1188.9 a	1390.3 a	898.6 a

Subtidal

Months	Treatment			
	Control, no border	Control, border	Cleared, no border	Cleared, border
0	1905.6 a	1994.4 a	0.0 b	0.0 b
1	2491.7 a	1936.1 b	334 c	48.4 c
2.5	1002.8 a	1227.8 a	366.8 b	6.7 c
5.5*	1933.3 a	2466.7 ab	1075 a	162.3 c
13	1958.3 a	2013.9 a	2111.1 a	1077.0 b

A.5 Statistical Analysis

Results of one-way ANOVA tests for mean seagrass species leaf production rates (g shoot^{-1} day^{-1}) versus quarterly sampling event Mabuiag Island.

Tested April 2011, July 2011 and October 2011.

*Enhalus acoroides**	DF	SS	MS	F	P
Between Quarters	1	0.000141	0.000141	0.133	0.7200
Residual	16	0.017	0.00106		
Total	17	0.0171			

* Data were square-root transformed to meet the assumption of normality

Tested April 2011, July 2011, October 2011, January 2012, May 2012 and July 2012.

Cymodocea rotundata	DF	SS	MS	F	P
Between Quarters	4	0.00911	0.00228	12.347	<0.001
Residual	24	0.00443	0.000184		
Total	28	0.0135			

Tested April 2011, July 2011, October 2011 and January 2012.

Halodule uninervis	DF	SS	MS	F	P
Between Quarters	2	0.00000107	0.000000536	16.834	<0.001
Residual	42	0.00000134	0.000000032		
Total	44	0.00000241			

Tested April 2011, July 2011, October 2011, January 2012 and May 2012.

Thalassia hemprichii	DF	SS	MS	F	P
Between Quarters	3	0.000094	0.0000313	11.288	<0.001
Residual	16	0.0000444	0.00000277		
Total	19	0.000138			

Results of Least Significant Difference (LSD; equal variances) or Behrens Fisher (unequal variances) pair-wise comparisons mean seagrass species leaf production rates (g shoot^{-1} day^{-1}) versus quarterly sampling event (April 2011, July 2011, October 2011, January 2012, May 2012 and July 2012), Mabuiag Island. Means that share a common letter for each month are not significantly different.

Quarter	*C. rotundata**	*H. uninervis*	*C. serrulata*	*S. isoetifolium**
April 2011	0.0274 a	0.000238 a	0.0363 a	0.000109 a
July 2011	0.0406 b	0.000349 ab		
October 2011	0.0681 c	0.000592 b	0.0506 b	0.000645 b
January 2011	0.0399 ab	0.000231 ab		
May 2012	0.0293 ab			
July 2012	0.0265		0.0402ab	

* Behrens Fisher comparison used.

Results of t-test for seagrass species leaf production rates (g shoot^{-1} day^{-1}) in April and October 2011, Mabuiag Island.

* Data were square-root transformed to meet the assumptions of normality

Syringodium isoetifolium	**DF**	**t**	**P**
Between Quarters	6	-5.816	0.0010