



# THE EFFECTS OF CLIMATE ON SEAGRASS IN THE TORRES STRAIT 2011-2014

Report No. 14/48  
November 2014



Carter, A.B., Taylor, H.A., McKenna, S.A.,  
York, P.Y., Rasheed, M.A.



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2011-2014

A Report for Torres Strait Regional Authority

Report No. 14/48

November 2014

Prepared by Alex Carter, Helen Taylor, Skye McKenna,  
Paul York and Michael Rasheed.

Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER)

James Cook University

PO Box 6811

Cairns Qld 4870

Phone : (07) 4781 4262

Email: [seagrass@jcu.edu.au](mailto:seagrass@jcu.edu.au)

Web: [www.jcu.edu.au/tropwater/](http://www.jcu.edu.au/tropwater/)

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**For further information contact:**

Alex Carter

Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER)

James Cook University

seagrass@jcu.edu.au

PO Box 6811

Cairns QLD 4870

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## EXECUTIVE SUMMARY

The Seagrass Ecology Group from James Cook University's Centre for Tropical Water & Aquatic Ecosystem Research (JCU TropWATER), in collaboration with the Torres Strait Regional Authority Land and Sea Management Unit (TSRA LSMU), established a research program from 2011 to 2014 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 environmental change. An intertidal seagrass monitoring site was established at Mabuiag Island where information on seagrass biomass and species composition, and environmental data including irradiance (light), global solar exposure, daytime tidal air exposure, mean and maximum daily water temperature, rainfall, wind speed and salinity, were collected.

Seagrasses at Mabuiag Island undergo distinct seasonal changes in biomass and species composition during summer, while biomass and species composition remain relatively stable between autumn and spring. Changes in biomass were driven by changes in total hours of daytime tidal exposure, maximum daily water temperature, mean daily irradiance and total rainfall in the 30 days prior to when biomass estimates were made. Changes in species composition were driven by total hours of daytime tidal air exposure, global solar exposure, and maximum daily water temperature. The negative effect of periods of peak maximum daily water temperature on seagrass growth indicates that Mabuiag Island's intertidal seagrasses already live at the upper limit of their thermal tolerance. Projected future increases in sea temperature are likely to have negative consequences for these shallow coastal meadows, 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 minimising any anthropogenic impacts to seagrass to ensure resilience to cumulative stressors of local seagrass populations remain high.

Results from this study highlight the importance of environmental drivers of seagrass change, and the benefits of monitoring over longer time periods to gain a more accurate understanding of seagrass dynamics. We recommend:

1. Commence a monitoring program of subtidal seagrass meadows for a similar time frame (3-4 years) to assess the relationship between subtidal seagrass biomass and species composition with environmental variables.
2. Commence manipulative experimental research to establish how Torres Strait seagrasses respond to some of the predicted effects of climate change, particularly to determine the thermal tolerance of different seagrass species found in Torres Strait.
3. Incorporate information collected from the present study and (1) and (2) to model the consequences of climate change on Torres Strait intertidal and subtidal seagrass to develop appropriate dugong and turtle management strategies that account for predicted changes in seagrass meadows.



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# 1 INTRODUCTION

The Torres Strait region covers an area of more than 35,000 km<sup>2</sup> 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 and economy. The health of marine resources to Torres Strait Islanders remains vital from a commercial, subsistence, and cultural point of view. Seagrass ecosystems are of particular importance to Torres Strait Islanders as they support fisheries, dugong and turtle populations, and drive 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 as one of the most valuable ecosystems globally (on a per hectare basis) for ecosystem services, preceded only by coral reefs and wetlands (Costanza et al. 2014). Torres Strait is estimated to contain between 13,425 km<sup>2</sup> (Coles et al. 2003) and 17,500 km<sup>2</sup> (Poiner and Peterkin 1996) of seagrass habitat, providing critical habitat for commercial and traditional fishery species, including a food source for dugong and turtle (Marsh and Kwan 2008; Sheppard et al. 2008; Coles et al. 2003). The dugong is the most significant and highest ranked traditional subsistence marine food source for Torres Strait Islanders (Kwan 2002; Johannes and MacFarlane 1991; Raven 1990; Nietschmann 1984), with evidence of subsistence use of dugongs in archaeological deposits dating back at least 7000 years (Wright 2011; Vanderwal 1973). The largest dugong population in the world is located in Torres Strait waters (Marsh and Lawler 2002; Marsh et al. 1997). A spatial model of dugong distribution based on aerial surveys (1987 - 2011) indicated the most important dugong habitat occurs in central Torres Strait and extends from Badu to Boigu Islands, east to Gerber (Gabba) Island and west to the Warul Kawa Island Indigenous Protected Area. This region contains 56% of the high and very high density dugong habitat in Torres Strait (Marsh et al. 2012). Seagrass surveys have also identified central Torres Strait as one of the most important regions of seagrass habitat in Queensland, with high above-ground productivity compared with other tropical seagrass communities (Taylor and Rasheed 2010; Chartrand et al. 2009; Rasheed et al. 2008).

Light, temperature, air exposure and nutrients affect biochemical processes of marine organisms, and are considered major factors controlling seagrass growth (Duarte et al. 2006; Mellors 2003). 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 often 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. Studies have shown substantial seagrass dieback of up to 60% on two occasions in central Torres Strait (Marsh et al. 2004; Long and Skewes 1996) that 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 turbidity from rivers on the south coast of Papua New Guinea are unlikely to affect seagrass communities of Torres Strait at such a large, regional scale (Daniell et al. 2006).

The dynamics of Torres Strait seagrasses are likely to be strongly influenced by environmental and climatic conditions. To date, however, no studies have examined the effect of multiple environmental drivers on seagrass change in this region. Understanding the dynamics of seagrass communities is critical knowledge when developing effective management strategies for dugong and turtle that depend on seagrass for food, and also in assessing how seagrasses in Torres Strait may be impacted by climate change. The Seagrass Ecology Group from James Cook University's Centre for Tropical Water & Aquatic Ecosystem Research (JCU TropWATER) in collaboration with the Torres Strait Regional Authority (TSRA) Land and Sea Management Unit (LSMU) launched a monitoring program from 2011 - 2014 at an intertidal seagrass meadow at

Mabuiag Island, Torres Strait, to provide critical information for the management of dugong and turtle in the Torres Strait by understanding how their key food resource, seagrass, is affected by environmental change.

The objectives of the seasonal seagrass monitoring study were to:

1. Conduct monitoring of seagrass biomass at intertidal sites to examine temporal variation in seagrass biomass and species composition;
2. Determine the effect of light, temperature, exposure, salinity, rainfall and wind speed on seagrass meadow biomass in intertidal meadows.



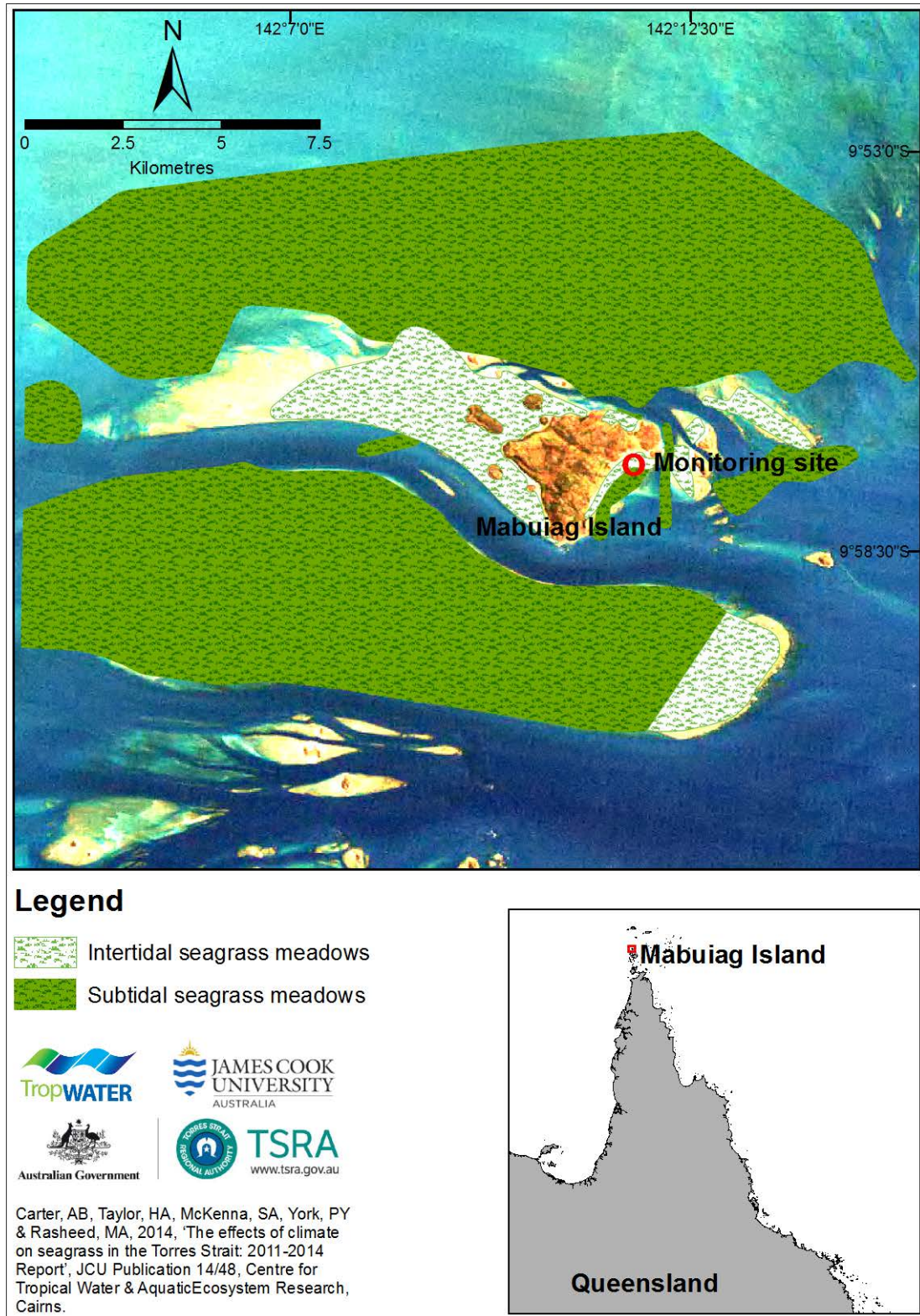
## 2 METHODS

### 2.1 Study location

Mabuiag Island is a continental island located in central Torres Strait, off the north-eastern tip of Australia. Surveys of intertidal and subtidal benthic habitats in the Mabuiag Island region conducted in 2009 and 2010 revealed extensive coverage of intertidal and subtidal seagrass meadows (Figure 1) (Taylor and Rasheed 2010; Chartrand et al. 2009). In May 2011, 18 permanent quadrats (0.25 m<sup>2</sup>) were established at an intertidal seagrass monitoring site (Figure 1) where the seagrass assemblage reflected 'typical' seagrass communities in the region. A further 18 permanent quadrats were established in October 2011. Unfortunately logistical and weather constraints prevented sampling all 36 quadrats during each sampling period (see Table 1). Between May 2011 and September 2012 seagrass was sampled approximately monthly, and between February 2013 and August 2014 seagrass was sampled quarterly.

**Table 1.** Permanent quadrat surveys undertaken between May 2011 and August 2014 including year, month and season of sampling. The number of quadrats sampled during a survey is in brackets.

Year	Season	Month ( <i>n</i> quadrats)
2011	Autumn	Early May (18)
	Autumn	Late May (18)
	Winter	June (18)
	Winter	July (18)
	Winter	August (18)
	Spring	September (18)
	Spring	October (36)
	Spring	November (36)
	2012	Summer
Summer		February (36)
Autumn		March (36)
Autumn		April (36)
Autumn		May (36)
Winter		June (36)
Winter		Early July (36)
Winter		Late July (30)
Winter		August (18)
Spring		September (18)
2013	Summer	February (36)
	Autumn	May (36)
	Winter	August (20)
	Spring	November (36)
2014	Summer	February (36)
	Autumn	May (36)
	Winter	August (36)



**Figure 1.** Map of intertidal seagrass monitoring site at Mabuia Island, Torres Strait, and distribution of intertidal and subtidal seagrass meadows in the Mabuia Island region.

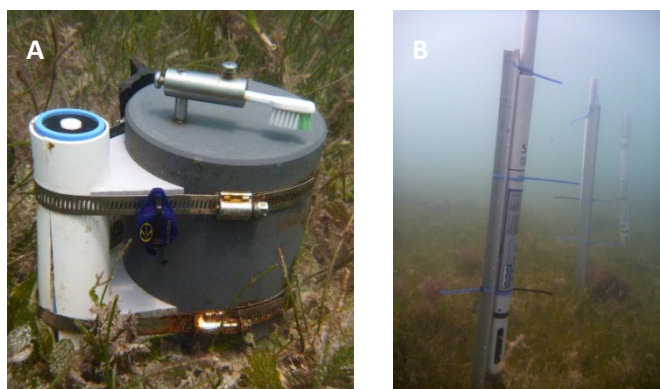
## 2.2 Seagrass biomass and species composition

Seagrass above-ground biomass and species composition were estimated for each quadrat using the “visual estimates of biomass” technique (Rasheed and Unsworth 2011; Mellors 1991). This technique involves an observer ranking seagrass biomass in the field in each quadrat while referring to a series of photographs of quadrats with similar seagrass habitats for which the above-ground biomass has been measured previously. 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 to above-ground biomass estimates in grams dry-weight per square metre ( $\text{g DW m}^{-2}$ ). At the completion of sampling each observer ranked a series of photographs of calibration quadrats representative of the range of seagrass biomass in the survey and where the seagrass had been harvested and  $\text{g DW m}^{-2}$  determined in the laboratory. A separate linear regression of ranks and biomass from these calibration quadrats was generated for each observer and applied to biomass calculations to account for differences in observers between sampling periods to determine above-ground biomass estimates.

## 2.3 Environmental monitoring

Environmental conditions in the seagrass meadow were recorded using three separate *in situ* loggers:

1. Autonomous iBTag submersible temperature loggers recorded water temperature ( $^{\circ}\text{C}$ ) within the seagrass canopy every 15 minutes (Figure 2a);
2. Submersible Odyssey<sup>TM</sup> photosynthetic irradiance (light) autonomous loggers recorded irradiance (measured as photosynthetically active radiation, PAR) every 15 minutes (Figure 2a); and
3. Submersible MX5 Sondes measured water temperature and salinity every 45 minutes (Figure 2b).



**Figure 2.** (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.

Tidal exposure to air for the meadow was calculated by summing the total daylight hours that tidal height was  $\leq 0.8\text{m}$  (the tidal height at which seagrass meadows expose at this location). Tidal data was provided by Maritime Safety Queensland (© The State of Queensland (Department of Transport and Main Roads) 2013, Tidal Data). Total global solar exposure (megajoules per square metre;  $\text{MJ m}^{-2} \text{ day}^{-1}$ ), total daily rainfall (mm), and wind speed (wind speed at midday,  $\text{km h}^{-1}$ ) 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/>).

## 2.4 Statistical analyses

Detailed descriptions of statistical analyses are provided in Appendix 1.

*Seagrass biomass* - Change in seagrass biomass among each combination of season and year was analysed using a Linear Mixed Effects Model (LME) with the “nlme” package (Pinheiro et al. 2007) in the statistical software environment R (v.3.1.1) (R Core Team 2014).

*Seagrass species composition* - Seagrass species biomass data was analysed using the multivariate statistical software package Primer-E Version 6 (Clarke and Gorley 2006) with a similarity matrix calculated using the Bray-Curtis coefficient on raw biomass data. Seagrass species composition was compared among seasons using analysis of similarities (ANOSIM) (Clarke and Gorley 2006). Similarity percentages-species contribution (SIMPER) analysis was used to explore the contribution made by individual species to dissimilarity in seagrass species composition among seasons (Clarke and Gorley 2006).

*Environmental variability* - For each of the 25 sampling periods total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean daily salinity, mean total daily irradiance, mean daily water temperature, and mean maximum daily water temperature were determined for the 30 days prior to the day that seagrass biomass was measured. Thirty days was selected to allow for a lag effect of environmental conditions on the meadow (Unsworth et al. 2012). Principal components analysis (PCA) was performed on normalised environmental data to reduce the number of dimensions of environmental data using Primer-E (Clarke and Gorley 2006).

*Environmental effects on seagrass biomass* - Generalized additive mixed models (GAMM) were used to examine the effects of environmental variables on seagrass biomass using the “mgcv” package for R (Wood 2014). Prior to fitting models the continuous covariates total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean daily salinity, mean total daily irradiance, mean daily water temperature, and mean maximum daily water temperature for the 30 days prior to measuring seagrass biomass were tested for collinearity using variance inflation factors (VIFs) with the “car” package (Fox and Weisberg 2011). Collinearity was high so mean daily water temperature (positive relationship with maximum daily water temperature, see Appendix 2), global solar exposure (positive relationship with irradiance, appendix 1), wind speed (negative relationship with rainfall and maximum daily water temperature; positive relationship with tidal exposure, Appendix 2) and mean salinity (negative relationship with maximum daily water temperature, positive relationship with tidal exposure, Appendix 2) were removed sequentially and VIFs recalculated each time. The VIFs of tidal exposure, irradiance, maximum daily water temperature, and rainfall were <2, indicating that collinearity was within reasonable limits and would not substantially inflate the standard errors of the model’s parameter estimates (Zuur et al. 2009).

*Environmental effects on seagrass species composition* - The relationship between environmental characteristics (total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean total daily irradiance, mean daily water temperature, and mean maximum daily water temperature) on seagrass species composition was examined using the Bioenvironmental Step (BEST) routine (Clarke and Gorley 2006).



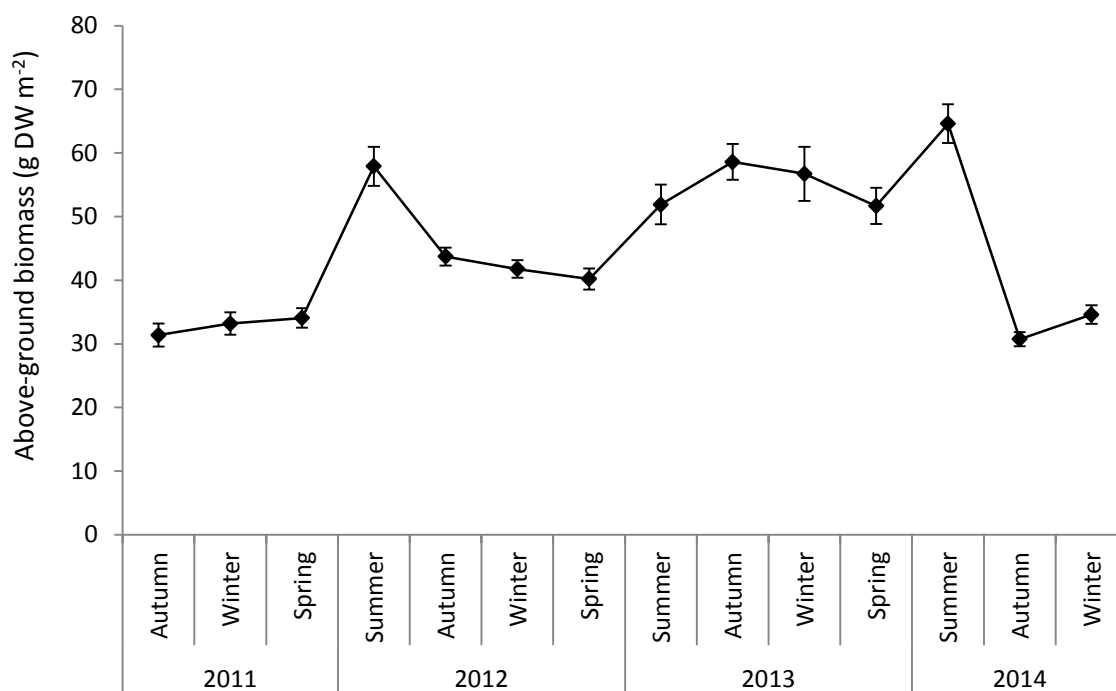
### 3 RESULTS

#### 3.1 Seagrass biomass

Seagrass biomass varied significantly among seasons and years (Table 2; Figure 3; Appendix 2). The intertidal meadow was characterised by relatively stable biomass between autumn, winter and spring within a calendar year (all  $p$ -values within a calendar year  $>0.05$ , Appendix 3), followed by a significant increase in biomass from spring to summer (all  $p$ -values  $< 0.01$ , Appendix 3). In 2012 and 2014, summer was the season of peak biomass and was followed by a significant decrease from summer to autumn (both  $p$ -values  $< 0.01$ , Appendix 2). This seasonal decline did not occur in 2013, however, and biomass remained high and stable ( $> 50$  g DW  $m^{-2}$ ) from summer to spring 2013 before increasing significantly again to  $65 \pm 3$  g DW  $m^{-2}$  in summer 2014 ( $p < 0.01$ ) (Figure 3). Biomass during the stable autumn to spring period was lowest in 2011 and 2014, ( $\sim 30$  g DW  $m^{-2}$ ) and greatest in 2013 ( $\sim 55$  g DW  $m^{-2}$ ; Figure 3).

**Table 2.** Results from a linear mixed effects model comparing seagrass biomass among sampling periods.

Fixed effect	NumDF	DenDF	F-value	P-value
(Intercept)	1	727	1346	$<0.0001$
Sampling period	13	727	31	$<0.0001$

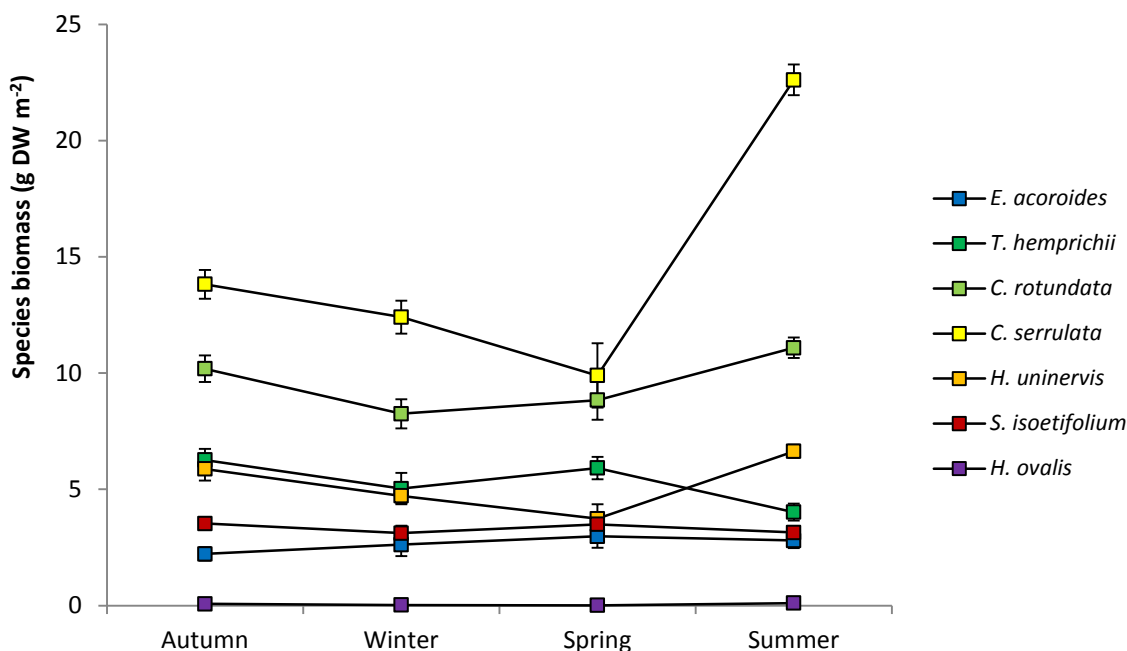


**Figure 3.** Average intertidal seagrass biomass ( $\pm$  standard error), autumn 2011 – winter 2014 at Mabuiag Island, Torres Strait.

#### 3.2 Seagrass species composition

Seven species of seagrass were recorded in the intertidal seagrass meadow at Mabuiag Island: *Cymodocea serrulata*, *C. rotundata*, *Thalassia hemprichii*, *Halodule uninervis*, *Syringodium isoetifolium*, *Enhalus acoroides*, and *Halophila ovalis*. Differences in seagrass species composition were found when sampling events were grouped into seasons (Figure 4) (ANOSIM  $R=0.052$ ;  $p=0.01$ ). Species composition in summer was significantly different to autumn, winter and spring (Figure 4; Table 3). Species composition in spring,

winter and autumn were similar (Figure 4; Table 3). Changes in species composition between summer and the other seasons (winter, spring and autumn) were driven mainly by increases in *C. serrulata*, *H. uninervis* and *C. rotundata*, and a decrease in *T. hemprichii* (Figure 4; Table 4). The low biomass species *H. ovalis* did not contribute to any of the differences between seasons.



**Figure 4.** Species-specific mean seagrass biomass ( $\pm$  standard error) for Mabuiag Island's intertidal meadow, measured across four seasons, March 2011 – August 2014.

**Table 3.** Analysis of similarity (ANOSIM) of species composition among four seasons.

Season comparison	<i>R</i> -statistic	<i>P</i> -value
Autumn v Winter	-0.002	0.66
Autumn v Spring	0.04	0.05
Autumn v Summer	0.09	<b>0.01</b>
Winter v Spring	0.04	0.06
Winter v Summer	0.08	<b>0.01</b>
Spring v Summer	0.13	<b>0.01</b>



**Table 4.** Species contributing to dissimilarity in seagrass species composition between autumn, winter and spring versus summer from SIMPER analysis. Species are listed in decreasing order of % contribution for each seasonal comparison.

Species	Autumn v Summer (average dissimilarity = 48.24)		
	Biomass autumn	Biomass summer	% Contribution
<i>C. serrulata</i>	13.82	26.05	34.35
<i>C. rotundata</i>	10.19	12.78	20.26
<i>H. uninervis</i>	5.88	7.64	15.27
<i>T. hemprichii</i>	6.26	4.63	12.73
<i>E. acoroides</i>	2.22	3.23	8.84
Winter v Summer (average dissimilarity = 48.79)			
	Biomass winter	Biomass summer	% Contribution
<i>C. serrulata</i>	13.7	26.05	35.75
<i>C. rotundata</i>	9.11	12.78	19.99
<i>H. uninervis</i>	5.21	7.64	14.03
<i>T. hemprichii</i>	5.55	4.63	11.73
<i>E. acoroides</i>	2.9	3.23	9.98
Spring v Summer (average dissimilarity = 52.31)			
	Biomass spring	Biomass summer	% Contribution
<i>C. serrulata</i>	11.14	26.05	35.59
<i>C. rotundata</i>	9.94	12.78	19.07
<i>T. hemprichii</i>	6.66	4.63	13.57
<i>H. uninervis</i>	4.2	7.64	13.48
<i>E. acoroides</i>	3.35	3.23	9.81

### 3.3 Environmental variability

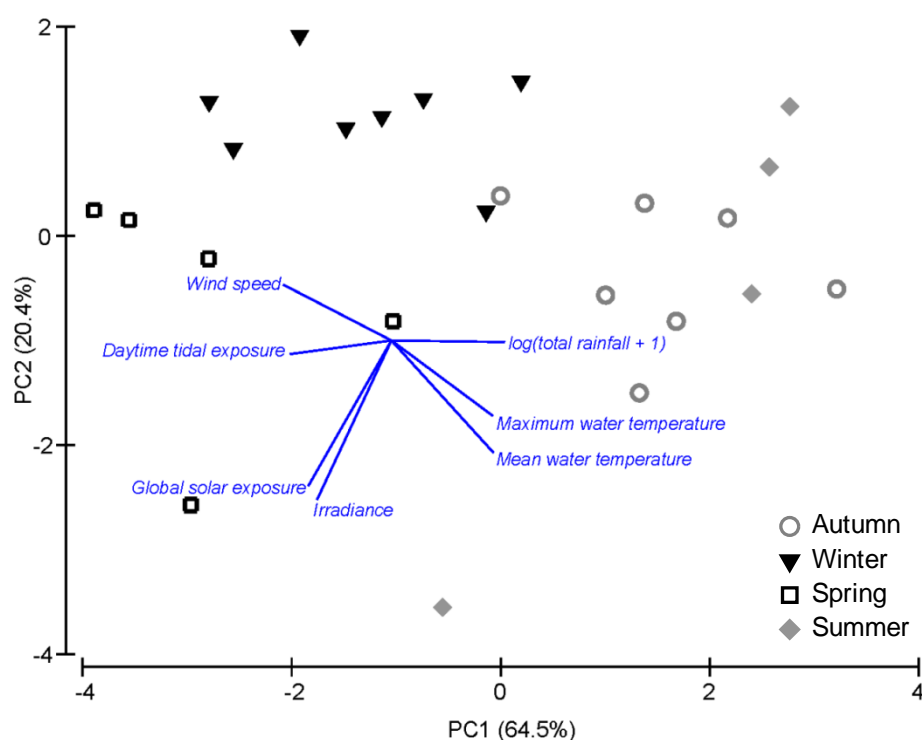
A distinct wet season (December – May; summer and autumn) and dry season (June – November; winter and spring) occurred in the Torres Strait during the study period. There was a strong grouping of sampling periods between the wet season and dry season with PC1 explaining 65% of variation in environmental data (Figure 5). Summer and autumn were associated with positive loadings of rainfall, mean water temperature and maximum water temperature along PC1, while winter and spring were associated with negative loadings on PC1 for wind speed and daytime tidal exposure (Figure 5). During the dry season little to no rainfall was recorded and salinity peaked (up to 41 ppt) (Figure 6). During the wet season total rainfall peaked (>100 mm) and salinity often fell below 32 ppt, particularly between February and April each year (Figure 6). Dry season sampling periods were also separated into winter and spring groupings along PC2 (20.4% of variation in environmental data explained), with winter sampling periods associated with high wind speed and spring sampling periods associated with high global solar exposure and irradiance (Figure 5).

Global solar exposure was on average  $20.3 \pm 0.2 \text{ MJ m}^{-2} \text{ day}^{-1}$ . Global solar exposure reached consistently high values in spring (>25  $\text{MJ m}^{-2} \text{ day}^{-1}$ ). During summer global solar exposure fluctuated between high values typical of spring, or very low values during peak rainfall periods during late summer and early autumn associated with high cloud cover (Figure 7a). The lowest global solar exposure measured was 1.7 (January 2014). The amount of irradiance reaching intertidal seagrass meadows, and available for use in seagrass photosynthesis, was highly variable. Irradiance was highest during spring (Figure 7b) when rainfall was lowest (Figure 6a), global solar exposure was highest (Figure 7a) and daytime tidal exposure was at a maximum (Figure 8). Mean total daily irradiance was  $15.3 \pm 0.2 \text{ mol m}^{-2} \text{ d}^{-1}$  and ranged from just under 1  $\text{mol m}^{-2} \text{ d}^{-1}$  to 39.0  $\text{mol m}^{-2} \text{ d}^{-1}$  (Figure 7b). The large range in irradiance at intertidal meadows was likely driven by tidal air exposure. A low tide at midday, for example, would have left seagrass meadows (and light

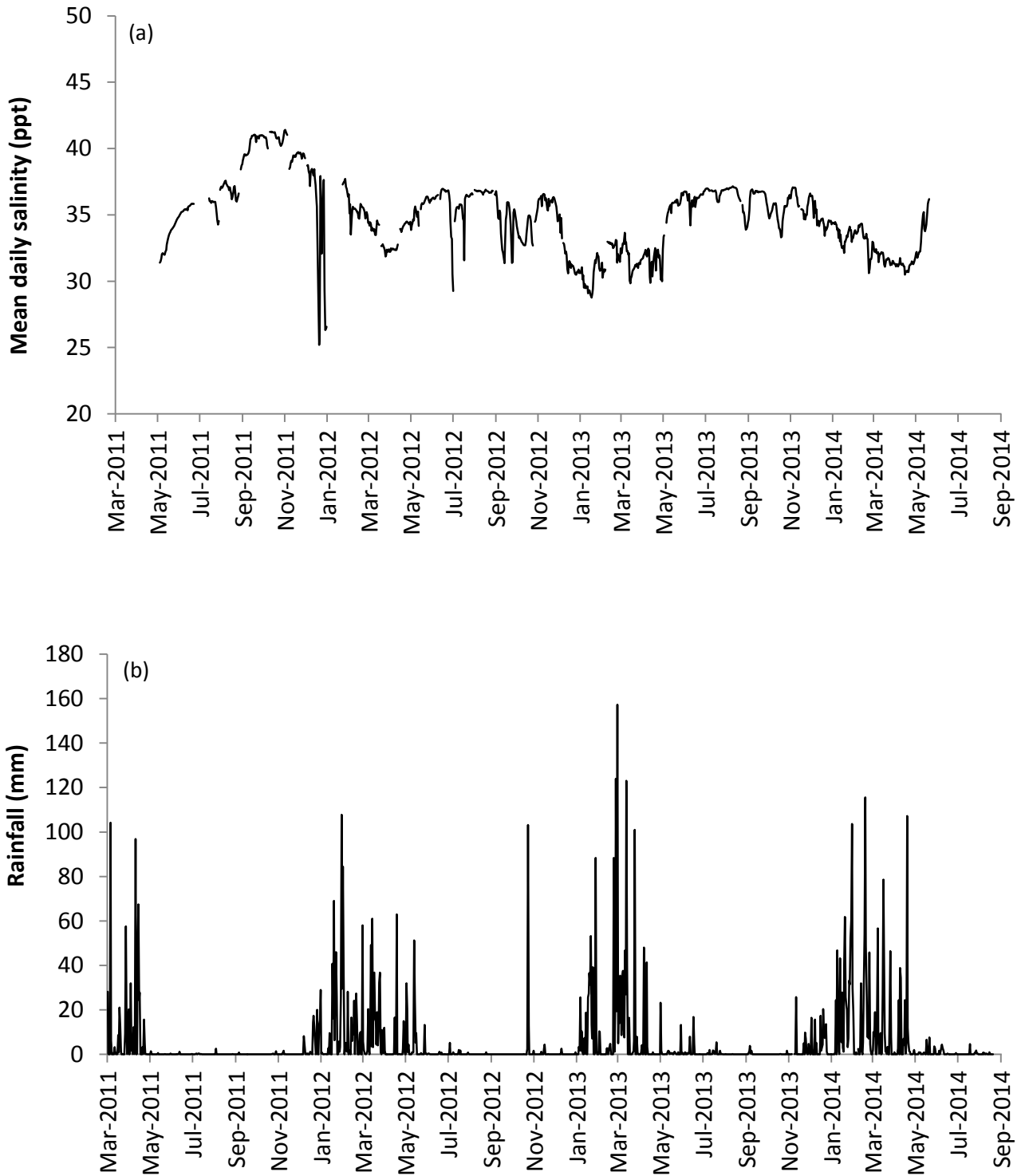
loggers) exposed during the time when sunlight was strongest, substantially increasing irradiance. Conversely, on a midday high tide seagrass meadows (and light loggers) would have been completely submerged and irradiance levels substantially reduced.

Intertidal seagrass meadows were exposed during daylight hours on low tide (1 - 7 days duration) for most spring tides during the 3.5 year monitoring period. Daytime tidal exposure duration ranged between 30 minutes and three hours each day (Figure 8a). Daytime tidal 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; Figure 8b). No daytime tidal exposure was recorded in December and January each year (summer), and exposure was minimal each February (approximately 0.5 – 1.5 hours daytime exposure; Figure 8b).

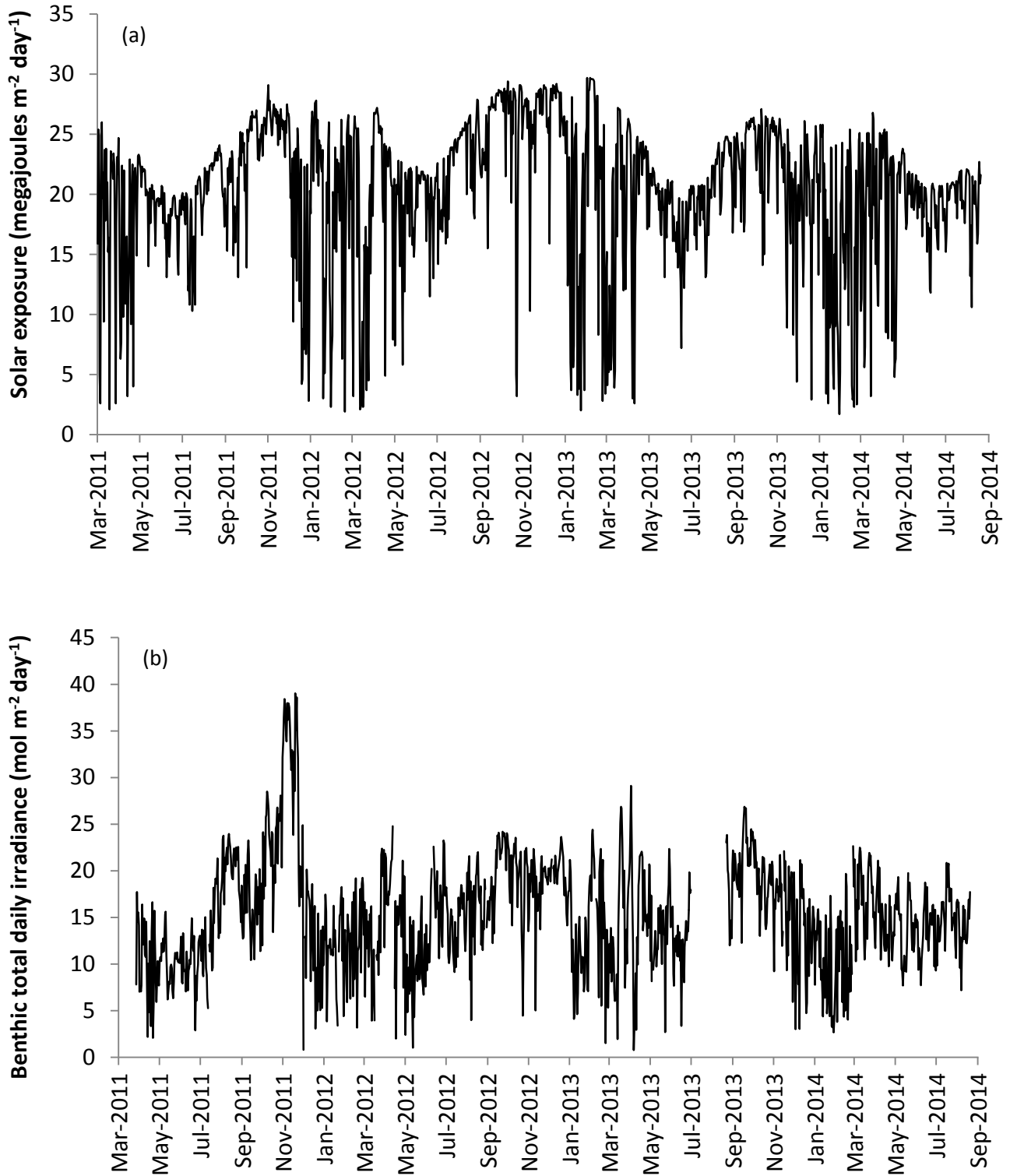
Periods of limited or no daytime tidal exposure coincided with summer peaks in mean and maximum water temperature (Figure 9a) and low wind speed (Figure 9b). Mean daily water temperature ranged from 24.1°C to 31.4°C, with an average of  $27.7 \pm 0.1^\circ\text{C}$ . Mean daily water temperature reached 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 (Figure 9a). Maximum water temperatures (>35°C) were recorded mid-March to mid-April. The coldest mean daily water temperatures (<25°C) were recorded late July through to early September each year. Maximum wind speed also occurred during winter and early spring, with midday wind speeds frequently >35 km h<sup>-1</sup> during this period (Figure 9b).



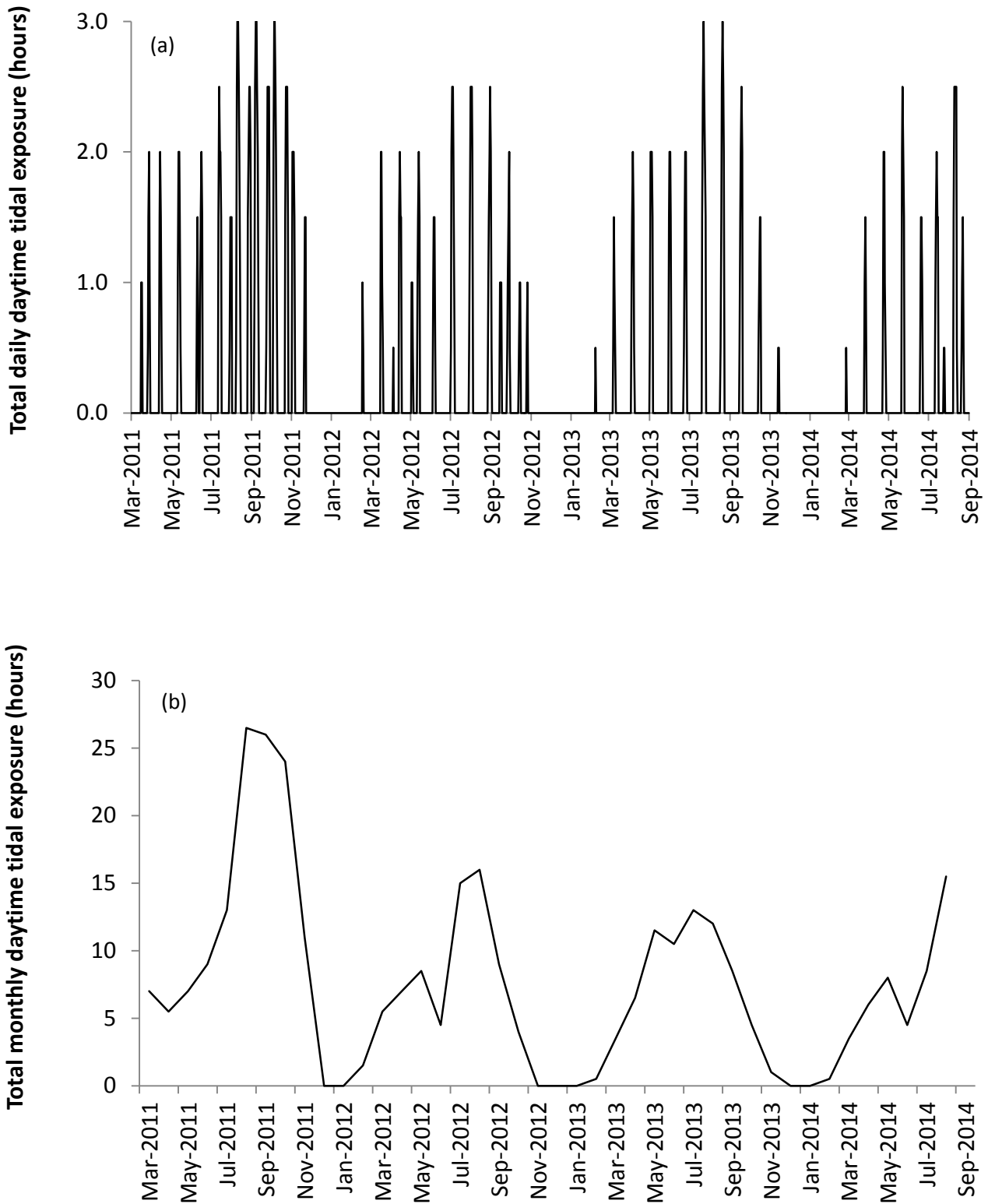
**Figure 5.** Principle components analysis of environmental variables at Mabuiag Island, Torres Strait. The 24 sampling periods are grouped by symbols representing winter and spring (dry season) and summer and autumn (wet season). Environmental variables total global solar exposure ( $\text{MJ m}^{-2} \text{ day}^{-1}$ ),  $\log(\text{total rainfall} + 1)$  (mm), mean daily water temperature ( $^\circ\text{C}$ ), maximum daily water temperature ( $^\circ\text{C}$ ), mean daily irradiance ( $\text{mol m}^{-2} \text{ day}^{-1}$ ), total daytime tidal exposure (hours), and wind speed ( $\text{km h}^{-1}$ ) were measured during 30 days prior to seagrass sampling. PC1 explained 64.5% percent variation and PC2 explained 20.4% variation.



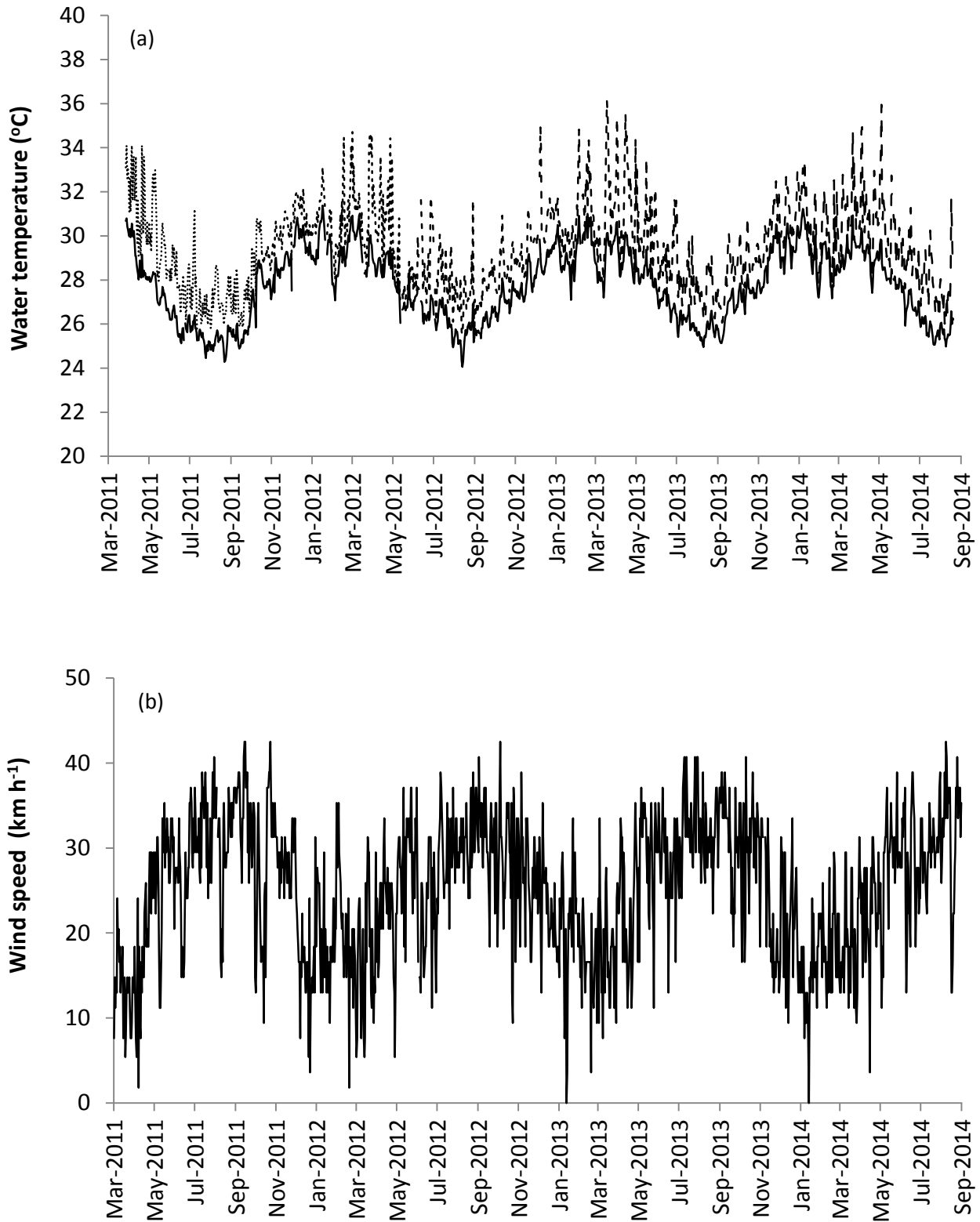
**Figure 6.** (a) Mean daily salinity (parts per thousand, ppt) at intertidal Mabuia Island seagrass meadows; and (b) total daily rainfall (mm) at Horn Island, Torres Strait, March 2011 – September 2014.



**Figure 7.** (a) Total daily global solar exposure (MJ m<sup>-2</sup> day<sup>-1</sup>) at Horn Island; and (b) total daily irradiance (mol m<sup>-2</sup> day<sup>-1</sup>) at intertidal Mabuig Island seagrass meadows, Torres Strait, March 2011 – September 2014.



**Figure 8.** (a) Total daily hours and (b) total monthly hours tidal exposure during daylight hours (0600-1800) at the Mabuiag Island intertidal seagrass meadow, Torres Strait, March 2011 – September 2014.



**Figure 9.** (a) Mean (solid line) and maximum (dashed line) daily water temperature (°C) at intertidal Mabuig Island seagrass meadows, Torres Strait; and (b) Daily midday wind speed (km h<sup>-1</sup>) at Horn Island, Torres Strait, March 2011 – September 2014.



### 3.4 Environmental effects on seagrass biomass and species composition

Variation in seagrass biomass was related to total daytime tidal air exposure, mean daily irradiance, water temperature and rainfall for the 30 days prior to each sampling event (Table 5). The effect of air exposure was that the highest seagrass biomass values coincided with minimal daytime tidal exposure, the lowest maximum daily water temperatures, and maximum irradiance and rainfall (Figure 11). When daytime tidal air exposure was 0 - 10 hours in the month biomass was greatest, when daytime tidal air exposure was 10 – 20 hours biomass declined, and beyond >20 hours daytime tidal air exposure biomass remained consistently low (Figure 11a). Seagrass biomass declined as maximum daily water temperature increased from 28 - 32°C, and remained at relatively low but consistent biomass when maximum daily water temperature was 32 - 36°C (Figure 11c). Seagrass biomass increased (although with some variation) with irradiance (Figure 11b), and there was a linear increase in seagrass biomass with total rainfall (Figure 11d).

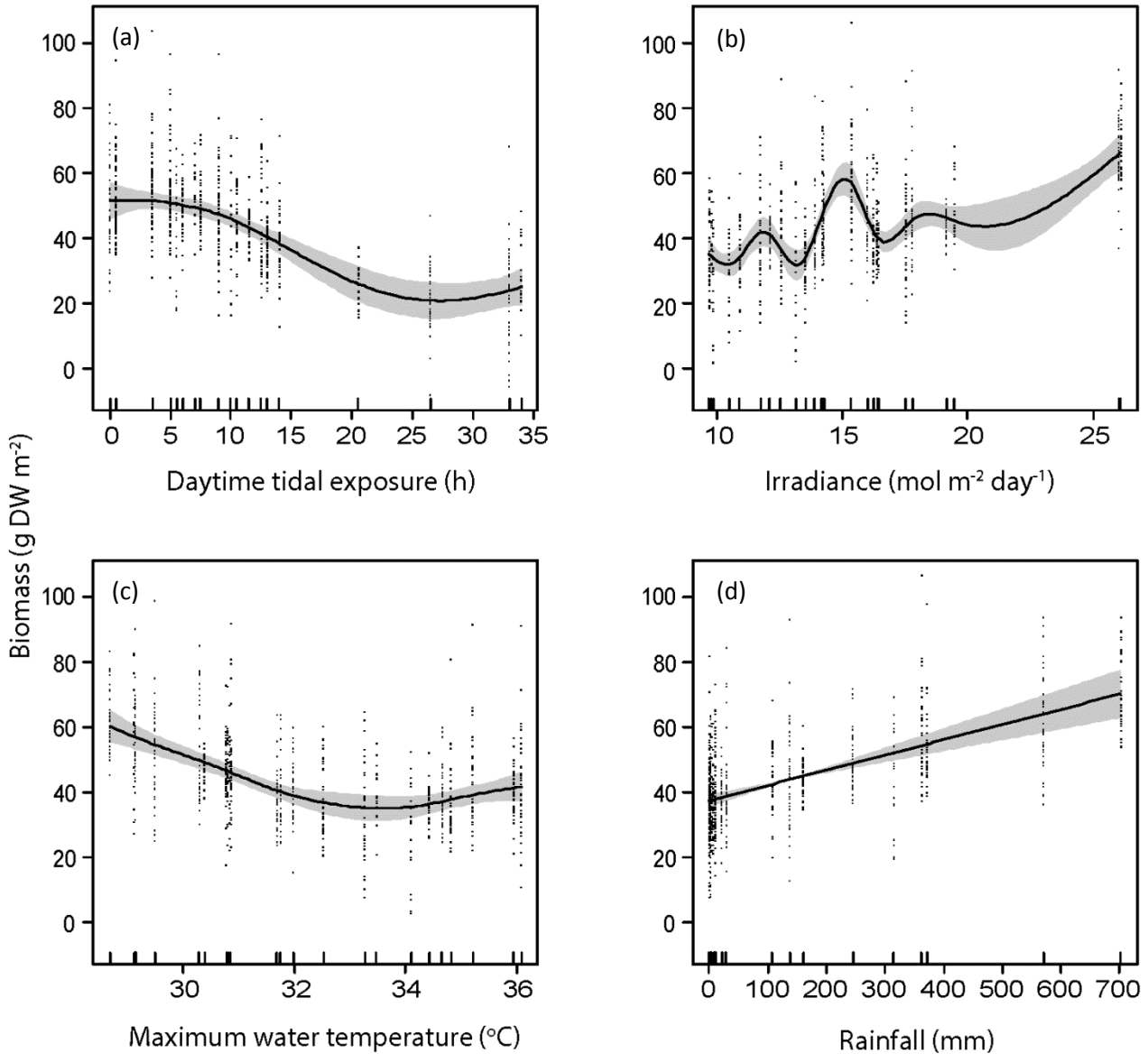
Many of the environmental variables were highly correlated (Appendix 1). This indicates that the predictors used in the selected model may be interchangeable with other environmental variables excluded from the analysis. For example, maximum daily water temperature is likely to be interchangeable with mean daily water temperature; global solar exposure with irradiance; daytime tidal exposure or maximum daily water temperature with salinity; and wind speed with rainfall, maximum daily water temperature, or daytime tidal exposure.

Seagrass species composition was shaped by similar environmental factors as those that determined biomass. Global solar exposure, maximum daily water temperature and daytime tidal exposure were the major factors affecting seagrass species composition (BEST analysis,  $Rho = 0.076$ ,  $p = 0.01$ ; Figure 11; Table 6).

**Table 5.** (a) Summary of generalized additive mixed model (GAMM) examining the continuous covariates total daytime tidal exposure ( $E$ , hours), mean daily irradiance ( $I$ ,  $\text{mol m}^{-2} \text{day}^{-1}$ ), mean maximum daily water temperature ( $MT$ , °C), and total rainfall ( $R$ , mm) on seagrass biomass ( $\text{g DW m}^{-2}$ ) at Mabuiag Island. Environmental values are based on the 30 days prior to measuring seagrass biomass. The selected model was considered to be the simplest model within two of the lowest  $AIC_c$ . (b) Overall fit of smooth terms of selected model including estimated degrees of freedom ( $edf$ ),  $F$ -statistic and  $p$ -values.

(a) Model	$AIC_c$	$\Delta AIC_c$	$w$	Adj. $R^2$
$Biomass = s(E) + s(I) + s(MT) + s(R) + \beta_{\text{quadrat}} + \varepsilon$	1628.1	0.00	0.48	0.31
(b) Smooth terms	$edf$	$F$	$p$ -value	
$s(E)$	3.74	28.65	$< 2^{-16}$	
$s(I)$	8.30	19.12	$< 2^{-16}$	
$s(MT)$	3.46	17.68	$5.20^{-12}$	
$S(R)$	1.00	51.49	$1.67^{-12}$	

$B_{\text{quadrat}}$  is the random effect of quadrat, and  $\varepsilon$  is the error term.  $AIC_c$  is the small-sample bias-corrected form of Akaike's information criterion;  $\Delta$  is the Akaike difference;  $w$  is the Akaike weight; Adj.  $R^2$  is adjusted coefficient of determination.



**Figure 11.** Predicted seagrass biomass ( $\text{g DW m}^{-2}$ ) at Mabuiag Island with changes in (a) total daytime tidal exposure (hours), (b) mean daily irradiance ( $\text{mol m}^{-2} \text{day}^{-1}$ ), (c) maximum daily water temperature ( $^{\circ}\text{C}$ ), and (d) total rainfall (mm) for the 30 days prior to measuring seagrass biomass. Non-linear trends are the fit of a Gaussian generalized additive mixed model (GAMM) with biomass as response. Grey areas are 95% confidence intervals.

**Table 6.** BEST variables explaining variation between seagrass species composition and environmental variables in the 30 days prior to sampling. Abbreviations: *GSE*, total global solar exposure ( $\text{MJ m}^{-2} \text{day}^{-1}$ ); *R*,  $\log(\text{total rainfall} + 1)$ ; *MnT*, mean daily water temperature ( $^{\circ}\text{C}$ ); *MT*, maximum daily water temperature ( $^{\circ}\text{C}$ ); *I*, irradiance ( $\text{mol m}^{-2} \text{day}^{-1}$ ); *E*, total daytime tidal exposure (hours); *W*, wind speed ( $\text{km h}^{-1}$ ).

No. variables	Correlation	Variable						
		<i>GSE</i>	<i>R</i>	<i>MnT</i>	<i>MT</i>	<i>I</i>	<i>E</i>	<i>W</i>
3	0.076	X			X		X	
2	0.073				X		X	
4	0.071	X	X		X		X	
2	0.070	X					X	
3	0.067	X	X				X	
3	0.067		X		X		X	
4	0.064	X			X	X	X	
5	0.061	X	X		X	X	X	
4	0.058	X		X	X		X	
3	0.058	X				X	X	

## 4 DISCUSSION

This is the first study to demonstrate the strong dependency of intertidal seagrass biomass and seagrass species composition on environmental conditions in Torres Strait. The Mabuiag Island seagrass meadow underwent a distinct change in summer where total biomass increased significantly and seagrass species composition changed, with increased dominance of *C. serrulata*, *C. rotundata* and *H. uninervis* and a decrease in *T. hemprichii*. Significant seasonality in tropical seagrass biomass has been previously reported for intertidal meadows at the nearby Orman Reefs, approximately 10 km northeast of Mabuiag Island, where a biomass reduction of 70% was recorded from March to November (Rasheed et al. 2008). In South East Asia seagrass biomass has been reported to vary by a factor of four (Lanyon and Marsh 1995; Erftemeijer and Herman 1994). Changes in biomass and species composition were driven by variation in daytime tidal air exposure and maximum daily water temperature, two collinear measures of light (irradiance for biomass and global solar exposure for species composition), and rainfall (although this was a much stronger driver of biomass than species composition).

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). Seagrass biomass peaked each summer following a period of steady increase in mean water temperature from ~24-26°C in July to ~28-30°C from December to February (Figure 9a). The positive effect of increasing water temperature (from 23°C to 29°C) on seagrass growth is well documented for many tropical seagrass species (Lee et al. 2007; Lee and Dunton 1996), indicating water temperature at Mabuiag Island from winter to summer is within the optimal range for tropical seagrass growth. Significant declines in seagrass biomass occurred between summer and autumn, however, with peaks in mean maximum water temperature in the preceding 30 days identified in this study as a contributing factor. Summer and autumn mean water temperatures were similar (~28-30°C), but fluctuations in maximum temperature were much greater in autumn and frequently exceeded 33°C. Seagrass biomass was suppressed when mean maximum water temperature was greater than 33°C (Figure 11). Inhibition of tropical seagrass growth has been recorded when temperatures reach a threshold of >35°C and thermally-induced physiological stress occurs (Collier and Waycott 2014; Rasheed and Unsworth 2011; Ralph 1998; Bulthuis 1983), although this threshold can be lower in temperate species (York et al. 2013). Declines in seagrass biomass when mean maximum water temperature is greater than 33°C suggest seagrasses at Mabuiag Island exceed their thermal maximum each autumn.

Peaks in maximum water temperature corresponded with the commencement of periods of daytime tidal air exposure, which also had a negative effect on seagrass biomass. Periods of no tidal air exposure that occurred during summer months likely buffered the intertidal meadow from the deleterious effects of “super-heating” of the thin layer of water covering the meadow during low tide events (Campbell et al. 2006). This phenomenon is likely to have contributed to declines in seagrass biomass from summer to autumn once mean maximum water temperatures exceed 33°C and seagrasses were also subjected to daytime tidal exposure. Super-heating during the cooler months in winter and spring is an unlikely explanation for reduced seagrass biomass as water temperature was at a minimum. The negative effect of daytime tidal exposure on meadow biomass was most likely due to desiccation and 'burning' (i.e. browning of the leaf material) when seagrasses became fully exposed (Unsworth et al. 2012). Burning was observed regularly in the intertidal region during winter and spring when peak periods of daytime tidal exposure coincided with peak wind speed (Figures 8, 9b). Studies of Indo-Pacific, north Queensland and southern China intertidal seagrass meadows have confirmed that long and frequent periods of daytime tidal exposure to air 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). It is noteworthy that seagrass biomass was lowest (~30 g DW m<sup>-2</sup>) during the autumn – spring exposure period in 2011, a year with greater daytime tidal exposure compared with 2012 and 2013 (Figures 3, 8).

The mechanisms by which exposure leads to seagrass decline are also often related to physiological stress to the leaf structure and photosystems by 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). This did not appear to be the case for Mabuiag Island's intertidal seagrasses, as seagrass biomass increased with irradiance (which was highly collinear with global solar exposure). The growth, survival and depth penetration of seagrass is directly related to the quality and quantity of light the meadow receives (Dennison 1987; Dennison and Alberte 1985). Light levels in Mabuiag Island's intertidal meadow were highly variable, but irradiance rarely fell below  $5 \text{ mol m}^{-2} \text{ d}^{-1}$  (Figure 7b) and mean irradiance in the 30 days prior to seagrass sampling was  $10 - 26 \text{ mol m}^{-2} \text{ d}^{-1}$ . These light levels likely well exceeded the minimum requirements for most tropical seagrass species (Chartrand et al. 2012; Collier et al. 2012). In our study there was little evidence of long term impacts of photo damage associated with high light levels: there was a peak in biomass in autumn 2013 when irradiance was  $15 \text{ mol m}^{-2} \text{ d}^{-1}$  (Figure 11). This was the highest irradiance recorded during autumn and the only year when seagrass biomass did not significantly decrease from summer to autumn, supporting the positive effect of light on seagrass biomass.

Rainfall had a significant positive correlation with seagrass biomass. The greatest biomass recorded ( $65 \pm 3 \text{ g DW m}^{-2}$ ) was in February 2014 following a month of heavy rainfall (700 mm in the 30 days preceding seagrass sampling), the highest rainfall recorded in a 30 day period in the 3.5 years of monitoring. Similar high biomass periods were recorded after 30 days of heavy rainfall in February 2012 ( $58 \pm 3 \text{ g DW m}^{-2}$ ; 570 mm) and February 2013 ( $52 \pm 3 \text{ g DW m}^{-2}$ ; 370 mm). The Mabuiag Island region lacks large river systems so increased rainfall does not lead to the large, freshwater pulses and increased turbidity seagrass meadows experience on Australia's east coast that can lower salinity and light to the point where seagrass growth is negatively impacted (Coles et al. 2014; 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 that salinity and light is reduced to the extent that growth is adversely affected.

Our results also suggest that changes in salinity may also be linked to seagrass changes in the Torres Strait. Tropical seagrasses typically live at the limit 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). Studies conducted on a limited number of seagrass species suggest most species have optimal growth when salinity is 30 - 40 ppt (Touchette 2007; Kahn and Durako 2006). Salinity was generally between 28 - 40 ppt at Mabuiag Island, within the known optimum range for seagrasses. However, in autumn – spring 2011 some of the lowest seagrass biomass periods coincided with the highest salinity levels recorded during this 3.5 year study (as well as the highest levels of daytime tidal exposure). During this period salinity frequently exceeded the 40 ppt (Figure 6a). Conversely peak seagrass biomass occurred in summer when rainfall was highest and salinity did not exceed 35 ppt, suggesting that the optimal salinity range for intertidal seagrass in Torres Strait may lie between 30 – 35 ppt.

## 5.1 Effects of predicted climate change

Seagrass meadows are being rapidly lost globally by 7% per year, with a third of global seagrass area lost since 1879 (Waycott et al. 2009). Continued declines in seagrass are mostly attributable to reductions in water quality from agricultural, urban and industrial runoff, port infrastructure and other coastal development, dredging, and storm damage (Grech et al. 2012; Waycott et al. 2009). Torres Strait seagrasses have remained largely insulated from these declines and the region continues to support some of the largest, healthiest and most diverse seagrass communities in the world. This insulation occurs because marine ecosystems in Torres Strait have been subjected to relatively low human impacts courtesy of low human population and watershed size in the region (Halpern et al. 2008). Global climate change, however, is predicted to negatively impact seagrass meadows worldwide (Harley et al. 2006). These impacts are likely to present significant challenges for management of marine resources in Torres Strait, as in other parts of the world. How Torres Strait seagrasses will respond to a changing climate and conditions for seagrass growth remains largely unknown. Predictions include elevated sea temperatures and sea levels, ocean acidification due to increased carbon dioxide concentrations, increased magnitude of tropical storm and cyclone events, and more extreme ENSO-related events such as droughts and floods (IPCC 2013; Pratchett et al. 2011; Short and Neckles 1999). To date, a lack of experimental studies that quantify the effects of climate change scenarios on Torres Strait seagrasses limits our ability to predict the consequences of climate change in this region, both for seagrass meadows and the fisheries and endangered species that depend on them.

There is scientific consensus that warming of the atmosphere and ocean has commenced and will continue (IPCC 2013). As water temperature rises, the distribution and density of species are likely to change depending on differing levels of thermal tolerance and adaptability (Harley et al. 2006). The negative effect of periods of elevated maximum water temperature at the Mabuiag Island seagrass meadow is of concern given projected future climate scenarios, with any increase in water temperature likely to have a deleterious impact on the productivity of this shallow coastal ecosystem. 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). Evidence suggests there is a critical temperature limit for seagrasses above which it is expected there would be a decrease in productivity and distribution (Short and Neckles 1999) due to direct effects on the balance between photosynthesis and respiration (Zimmerman et al. 1989; Bulthuis 1987; Evans et al. 1986; Marsh et al. 1986). Mabuiag Island's intertidal seagrass biomass decreased during a 30 day period of maximum water temperatures hovering in the 33-36°C range, indicating that at times seagrasses are already experiencing declines due to high water temperatures, a scenario likely to be more common under predicted climate change models. Seagrass responses to changes in water temperature are likely to result in changes in seasonal and geographic patterns of biomass, distribution and species composition (Walker 1991; McMillan 1984). The effect of increased temperature will depend on the individual species' thermal tolerances and optimum temperatures for photosynthesis, respiration and growth. Increased water temperature is likely to have particularly negative consequences for the Mabuiag Island meadow biomass and changes in species composition as the species most vulnerable to elevated water temperatures (*C. serrulata*, *C. rotundata*, *H. uninervis*) were also the most dominant species in the meadow.

The negative effect of daytime tidal exposure to air is likely to be particularly pronounced when coupled with increases in air temperature. Projected increases in air temperature are likely to have significant effects on coastal intertidal seagrass meadows (Waycott et al. 2007). Increased air temperature is likely to be particularly deleterious to Torres Strait's intertidal seagrass meadows when coupled with periods of daytime tidal exposure that already place multiple stresses on seagrass meadows, including spikes in water temperature, desiccation during air exposure, and increased salinity due to evaporation. The negative effects of daytime tidal exposure may be further exacerbated by sea level rise in the Torres Strait, with a projected rise of 0.84m by 2100 (Suppiah et al. 2007). Sea level rise is expected to cause a change in the magnitude of tidal range; depending on coastal geomorphology and the degree of tidal restriction already existing at a given location, expansion or lessening of tidal range may occur (De Jonge and De Jong 1992). A



lessening of tidal range may mitigate against the negative effects of daytime air exposure on intertidal meadows, but when combined with sea level rise may lead to reductions in light that negatively impact shallow water species that require high light environments for optimal growth such as *Thalassia* and *Cymodocea* spp. (Waycott et al. 2007). Alternatively, any expansion of tidal range and frequency or severity of exposure events would likely cause a reduction in seagrass biomass and changes in species composition. This is because an increase in the frequency or severity of exposure events favours smaller species with faster recovery times such as *Halodule* and *Halophila* spp. (Waycott et al. 2007). At Mabuiag Island these species formed a relatively minor proportion of total biomass relative to the larger and more abundant species *C. serrulata*, *C. rotundata* and *T. hemprichii*, and to a lesser extent *E. acoroides*.

Mabuiag Island's intertidal seagrass meadow benefited from elevated rainfall over a period of 30 days, most likely due to the increase in nutrients from run-off; however, meadow biomass also benefited from periods of high light. The intensity of cyclones and major storms is predicted to increase in the next 100 years and with this, more extreme pulse rainfall events (Poloczanska et al. 2007; Waycott et al. 2007). Typical environmental conditions during flooding and severe storm events, such as strong winds, turbulent water flow, storm surge, increased rainfall and increased sediment movement, can be detrimental for coastal seagrass due to reductions in light required for growth and sediment movement that can either bury or dislodge plants, meadows, and seed banks (Waycott et al. 2007). Flooding and storm events in 2010-2011 have been linked to significant seagrass loss in shallow coastal habitats on Queensland's east coast (Coles et al. 2014). Recent findings indicate recovery from an episodic loss of seagrass at Mabuiag Island is likely to take anywhere from several months (assuming asexual reproduction is possible), to several years if total meadow loss occurred and recovery relied only on sexual reproduction (Taylor et al. 2013).

## 5.2 Management implications

Potential changes in Torres Strait seagrass communities due to climate change may have profound implications for dugong and turtle populations, and economically important fisheries. The spatial distribution of seagrass as a quality food source 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 a 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.

The management of Torres Strait seagrass resources should be focused on minimizing any anthropogenic impacts and risks to ensure resilience of local seagrass populations remain high by reducing the cumulative effects of multiple stressors as much as possible. 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 (e.g. Mourilyan Harbour; Reason et al. (2012)). At present, seagrass species that are confirmed food for dugong, *H. uninervis* and *H. ovalis*, have high levels of resilience with dense seed banks established and an ability to rapidly re-colonise disturbed areas using sexual and asexual means (Taylor et al. 2013). Many other species found in the Torres Strait 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 (Taylor et al. 2013).

Changes in seagrass distribution and species composition may result in changes in dugong feeding areas. Flexibility may be required in the management of Torres Strait seagrass and dugong to accommodate future change, rather than a reliance on fixed spatial closures and management areas that are not easily modified.

Results from the research recommended in the following section will place resource managers in Torres Strait in a better position to anticipate where seagrass change may occur, and decide how best to incorporate change into future management plans.

### **5.3 Recommendations**

This study provides a valuable baseline of natural variation in an intertidal seagrass meadow in Torres Strait, and the response of that meadow to environmental factors. A shift in focus of the monitoring and research program from Mabuiag Island intertidal seagrass meadows will gather further information on how natural climate variability affects subtidal seagrass, and how future scenarios of climate change are likely to impact seagrass meadows and, therefore, dugong and turtle feeding opportunities. We recommend:

1. Commence a monitoring program of subtidal seagrass meadows for a similar time frame (3-4 years) to assess the relationship between subtidal seagrass biomass and species composition with environmental variables.
2. Commence manipulative experimental research to establish how Torres Strait seagrasses respond to some of the predicted effects of climate change, particularly to determine the thermal maximum of different seagrass species found in Torres Strait.
3. Incorporate information collected from the present study and (1) and (2) to model the consequences of climate change on Torres Strait intertidal and subtidal seagrass to develop appropriate dugong and turtle management strategies that account for predicted changes in seagrass meadows.

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## 7 APPENDICES

### Appendix 1.

#### Statistical analyses

##### *Seagrass biomass*

Change in seagrass biomass among each combination of season and year was analysed using a Linear Mixed Effects Model (LME) with the “nlme” package (Pinheiro et al. 2007) in the statistical software environment R (v.3.1.1) (R Core Team 2014). Mixed effects models allow for the separation of explanatory variables into random (unplanned) and fixed (planned) effects. The fixed effect was each combination of season and year. Quadrat was modelled as a random effect term in the model to eliminate potential bias resulting from the non-independence of biomass data collected from the same quadrats. The error part of the models were separated into a random component described by Gaussian temporally autocorrelated errors using cor AR1, and a normally distributed error term. A Tukey post hoc comparison with Holm adjustment was used for pairwise comparisons of biomass between each season-year combination using the “multcomp” package in R (Hothorn et al. 2008). Models were validated by plotting standardised residuals against fitted values and also against each explanatory variable to assess homogeneity and independence. Normality of residuals was also verified using qq-plots (Pinheiro and Bates 2000).

##### *Seagrass species composition*

Seagrass species biomass data was analysed using the multivariate statistical software package Primer-E Version 6 (Clarke and Gorley 2006) with a similarity matrix calculated using the Bray-Curtis coefficient on raw biomass data. Seagrass species composition was compared among seasons using analysis of similarities (ANOSIM) (Clarke and Gorley 2006) with a maximum of 999 permutations with pairwise comparisons used to identify differences between groups. Similarity percentages-species contribution (SIMPER) analysis was used to explore the contribution made by individual species to dissimilarity in seagrass species composition among seasons as determined by (Clarke and Gorley 2006).

##### *Environmental variability*

For each of the 25 sampling periods total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean daily salinity, mean total daily light (irradiance), mean daily water temperature, and mean maximum daily water temperature were determined for the 30 days prior to the day that seagrass biomass was measured. Thirty days was selected to allow for a lag effect of environmental conditions on the meadow (Unsworth et al. 2012).

Principal components analysis (PCA) was performed on normalised environmental data to reduce the number of dimensions of environmental data using Primer-E (Clarke and Gorley 2006). Prior to PCA rainfall data was  $\log(\text{biomass}+1)$  transformed and a similarity matrix was calculated using a Euclidean distance coefficient. Salinity was not included in the analysis due to several sampling periods with missing data. August 2013 was also excluded from the environmental analysis due to missing light data.

##### *Environmental effects on seagrass biomass*

Generalized additive mixed models (GAMM) were used to examine the effects of environmental variables on seagrass biomass using the “mgcv” package for R (Wood 2014). GAMMs were used because the functional form of the response variable biomass to the continuous environmental covariates was unknown; GAMMs fit a non-parametric model to the data where the functional form is not specified *a priori*, but instead additive non-parametric functions are estimated using smoothing splines to model

covariates (Zuur et al. 2014). Prior to fitting models the continuous covariates total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean daily salinity, mean total daily irradiance, mean daily water temperature, and mean maximum daily water temperature for the 30 days prior to measuring seagrass biomass were tested for collinearity using variance inflation factors (VIFs) with the “car” package (Fox and Weisberg 2011). Collinearity was high so mean daily water temperature (positive relationship with maximum daily water temperature, see Appendix 1), global solar exposure (positive relationship with irradiance, Appendix 1), wind speed (negative relationship with rainfall and maximum daily water temperature; positive relationship with tidal exposure, appendix 1) and mean salinity (negative relationship with maximum daily water temperature, positive relationship with tidal exposure, Appendix 1) were removed sequentially and VIFs recalculated each time. The VIFs of tidal exposure, irradiance, maximum daily water temperature, and rainfall were <2, indicating that collinearity was within reasonable limits and would not substantially inflate the standard errors of the model’s parameter estimates (Zuur et al. 2009).

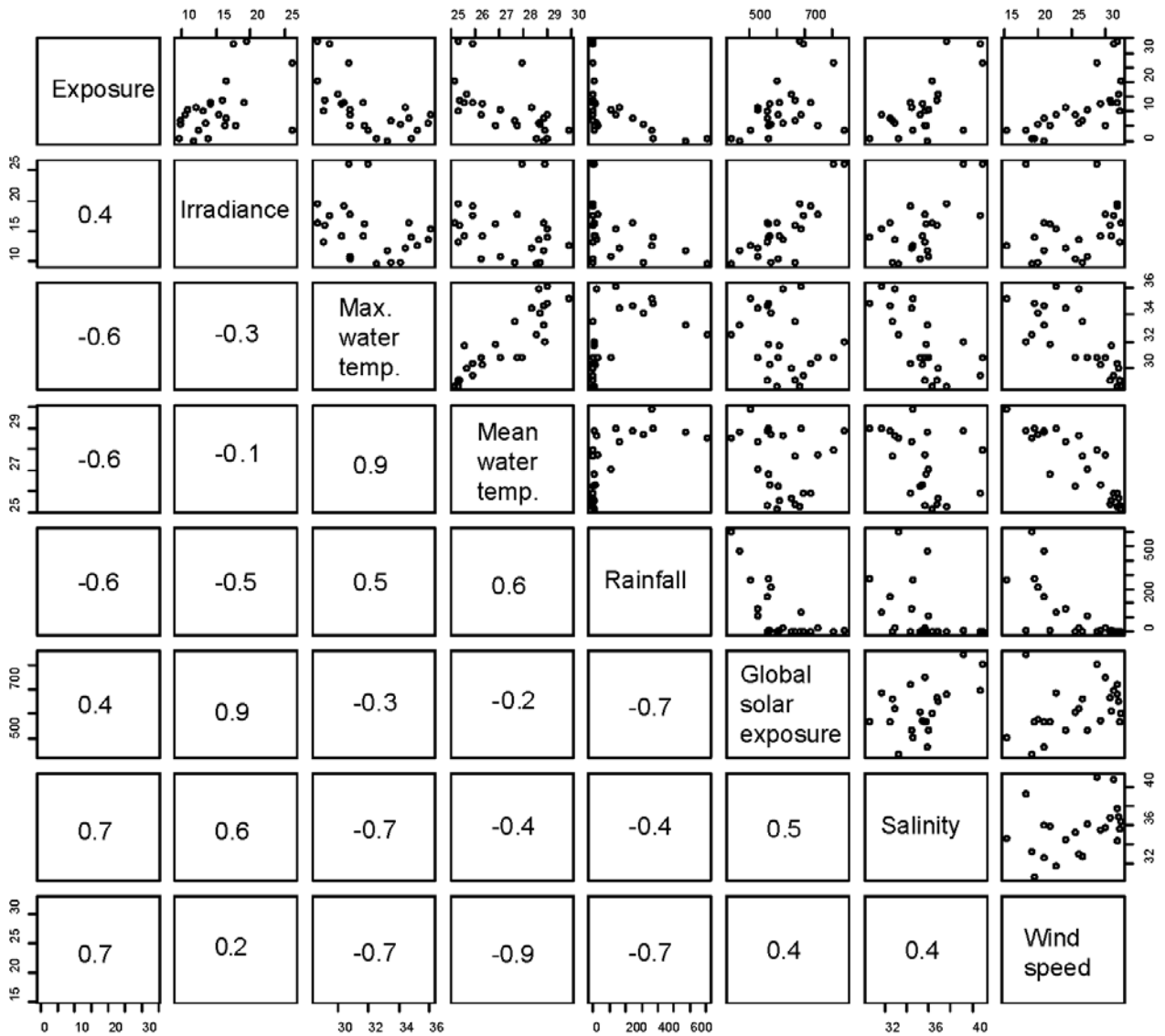
To determine the optimal model, a global model for seagrass biomass was created where tidal exposure, irradiance, maximum daily water temperature, and total rainfall were modelled with smoothing splines. Sub-model sets of the global model were generated using the dredge function in the MuMIn package (Barton 2013). The best-fit model was considered to be the simplest model with the lowest Akaike’s Information Criterion corrected for small sample sizes (AICc) that fell within two of the lowest AICc (Burnham and Anderson 2002). As with the LME analysis, quadrat was modelled as a random effect term and the error part of the model was separated into a random component described by Gaussian temporally autocorrelated errors using cor AR1, and a normally distributed error term. Normalised residuals were inspected for the best-fit final model using residual plots and qq-plots for violations of the assumptions of homogeneity of variance and normality (Zuur et al. 2014).

#### *Environmental effects on seagrass species composition*

The relationship between environmental characteristics (total global solar exposure, total rainfall, total daytime tidal exposure, mean wind speed, mean total daily irradiance, mean daily water temperature, and mean maximum daily water temperature) on seagrass species composition was examined using the Bioenvironmental Step (BEST) routine (Clarke and Gorley 2006). The BEST analysis, run 999 permutations to correlate multivariate species assemblage data with environmental variables using Spearman’s rank coefficient to determine which variable or which combination of predictors best explains community structure. Salinity was not included in the analysis due to several sampling periods with missing data. August 2013 was also excluded from the BEST analysis due to missing irradiance data.

**Appendix 2.**

Scatterplot matrix of correlations between environmental variables 30 days prior to seagrass sampling in the Mabuiag Island intertidal meadow. Values in bottom left portion of figure are Pearson correlation coefficients.



**Appendix 3.**

Tukey's post-hoc comparison with Holm adjustment comparing seagrass biomass among each combination of season and year. Significance codes: \*\*\* = 0.001, \*\* = 0.01, \* = 0.05, Ns = not significant ( $p > 0.05$ ).

Time 1 v Time 2		Estimate	Std. Error	z value	Pr(> z )	Sig.
Autumn.2012	Autumn.2011	12.6522	2.8267	4.476	<0.01	***
Autumn.2013	Autumn.2011	27.1917	3.3429	8.134	<0.01	***
Autumn.2014	Autumn.2011	-0.652	3.3429	-0.195	1	Ns
Spring.2011	Autumn.2011	2.5512	2.8772	0.887	0.9998	Ns
Spring.2012	Autumn.2011	7.15	3.3352	2.144	0.6551	Ns
Spring.2013	Autumn.2011	20.2828	3.3429	6.067	<0.01	***
Summer.2012	Autumn.2011	28.0681	2.9762	9.431	<0.01	***
Summer.2013	Autumn.2011	20.4398	3.3428	6.115	<0.01	***
Summer.2014	Autumn.2011	33.2143	3.3429	9.936	<0.01	***
Winter.2011	Autumn.2011	1.7739	3.0153	0.588	1	Ns
Winter.2012	Autumn.2011	11.2301	2.7437	4.093	<0.01	**
Winter.2013	Autumn.2011	24.6971	3.9515	6.25	<0.01	***
Winter.2014	Autumn.2011	3.1972	3.3429	0.956	0.9995	Ns
Autumn.2013	Autumn.2012	14.5395	2.6798	5.426	<0.01	***
Autumn.2014	Autumn.2012	-13.3042	2.6798	-4.965	<0.01	***
Spring.2011	Autumn.2012	-10.101	2.088	-4.838	<0.01	***
Spring.2012	Autumn.2012	-5.5021	2.6672	-2.063	0.7128	Ns
Spring.2013	Autumn.2012	7.6306	2.6798	2.847	0.1899	Ns
Summer.2012	Autumn.2012	15.4159	2.1461	7.183	<0.01	***
Summer.2013	Autumn.2012	7.7876	2.6793	2.907	0.1656	Ns
Summer.2014	Autumn.2012	20.5621	2.6798	7.673	<0.01	***
Winter.2011	Autumn.2012	-10.8782	2.3932	-4.546	<0.01	***
Winter.2012	Autumn.2012	-1.4221	1.8419	-0.772	1	Ns
Winter.2013	Autumn.2012	12.0449	3.3658	3.579	0.0224	*
Winter.2014	Autumn.2012	-9.455	2.6798	-3.528	0.0266	*
Autumn.2014	Autumn.2013	-27.8436	3.2193	-8.649	<0.01	***
Spring.2011	Autumn.2013	-24.6405	2.7493	-8.962	<0.01	***
Spring.2012	Autumn.2013	-20.0416	3.1893	-6.284	<0.01	***
Spring.2013	Autumn.2013	-6.9089	3.197	-2.161	0.643	Ns
Summer.2012	Autumn.2013	0.8765	2.8381	0.309	1	Ns
Summer.2013	Autumn.2013	-6.7519	3.0233	-2.233	0.588	Ns
Summer.2014	Autumn.2013	6.0226	3.217	1.872	0.8316	Ns
Winter.2011	Autumn.2013	-25.4177	2.9853	-8.514	<0.01	***
Winter.2012	Autumn.2013	-15.9616	2.5911	-6.16	<0.01	***
Winter.2013	Autumn.2013	-2.4946	3.6453	-0.684	1	Ns
Winter.2014	Autumn.2013	-23.9945	3.2196	-7.453	<0.01	***
Spring.2011	Autumn.2014	3.2032	2.7493	1.165	0.9964	Ns
Spring.2012	Autumn.2014	7.802	3.2117	2.429	0.4425	Ns
Spring.2013	Autumn.2014	20.9348	3.1971	6.548	<0.01	***
Summer.2012	Autumn.2014	28.7201	2.8381	10.12	<0.01	***
Summer.2013	Autumn.2014	21.0918	3.2195	6.551	<0.01	***



Summer.2014	Autumn.2014	33.8662	3.0234	11.201	<0.01	***
Winter.2011	Autumn.2014	2.4259	2.9853	0.813	0.9999	Ns
Winter.2012	Autumn.2014	11.8821	2.5921	4.584	<0.01	***
Winter.2013	Autumn.2014	25.349	3.8074	6.658	<0.01	***
Winter.2014	Autumn.2014	3.8492	3.0234	1.273	0.9916	Ns
Spring.2012	Spring.2011	4.5988	2.74	1.678	0.9174	Ns
Spring.2013	Spring.2011	17.7316	2.7493	6.449	<0.01	***
Summer.2012	Spring.2011	25.5169	2.221	11.489	<0.01	***
Summer.2013	Spring.2011	17.8886	2.7492	6.507	<0.01	***
Summer.2014	Spring.2011	30.6631	2.7493	11.153	<0.01	***
Winter.2011	Spring.2011	-0.7773	2.4559	-0.316	1	Ns
Winter.2012	Spring.2011	8.6789	1.9777	4.388	<0.01	***
Winter.2013	Spring.2011	22.1459	3.4295	6.457	<0.01	***
Winter.2014	Spring.2011	0.646	2.7493	0.235	1	Ns
Spring.2013	Spring.2012	13.1327	3.2114	4.089	<0.01	**
Summer.2012	Spring.2012	20.9181	2.8289	7.394	<0.01	***
Summer.2013	Spring.2012	13.2898	3.0168	4.405	<0.01	***
Summer.2014	Spring.2012	26.0642	3.2117	8.116	<0.01	***
Winter.2011	Spring.2012	-5.3761	2.9768	-1.806	0.8646	Ns
Winter.2012	Spring.2012	4.0801	2.511	1.625	0.9347	Ns
Winter.2013	Spring.2012	17.547	3.8007	4.617	<0.01	***
Winter.2014	Spring.2012	-3.9529	3.2117	-1.231	0.9939	Ns
Summer.2012	Spring.2013	7.7853	2.8381	2.743	0.242	Ns
Summer.2013	Spring.2013	0.157	3.2168	0.049	1	Ns
Summer.2014	Spring.2013	12.9315	3.0234	4.277	<0.01	**
Winter.2011	Spring.2013	-18.5088	2.9853	-6.2	<0.01	***
Winter.2012	Spring.2013	-9.0527	2.5921	-3.492	0.0293	*
Winter.2013	Spring.2013	4.4143	3.6453	1.211	0.9948	Ns
Winter.2014	Spring.2013	-17.0856	3.217	-5.311	<0.01	***
Summer.2013	Summer.2012	-7.6283	2.8379	-2.688	0.2725	Ns
Summer.2014	Summer.2012	5.1461	2.8381	1.813	0.8615	Ns
Winter.2011	Summer.2012	-26.2942	2.5682	-10.238	<0.01	***
Winter.2012	Summer.2012	-16.838	2.0972	-8.029	<0.01	***
Winter.2013	Summer.2012	-3.3711	3.4936	-0.965	0.9995	Ns
Winter.2014	Summer.2012	-24.8709	2.8381	-8.763	<0.01	***
Summer.2014	Summer.2013	12.7745	3.2192	3.968	<0.01	**
Winter.2011	Summer.2013	-18.6659	2.9852	-6.253	<0.01	***
Winter.2012	Summer.2013	-9.2097	2.5837	-3.565	0.0235	*
Winter.2013	Summer.2013	4.2573	3.7905	1.123	0.9975	Ns
Winter.2014	Summer.2013	-17.2426	3.2195	-5.356	<0.01	***
Winter.2011	Summer.2014	-31.4403	2.9853	-10.532	<0.01	***
Winter.2012	Summer.2014	-21.9841	2.5921	-8.481	<0.01	***
Winter.2013	Summer.2014	-8.5172	3.7906	-2.247	0.5793	Ns
Winter.2014	Summer.2014	-30.0171	3.1971	-9.389	<0.01	***
Winter.2012	Winter.2011	9.4562	2.2945	4.121	<0.01	**
Winter.2013	Winter.2011	22.9231	3.6259	6.322	<0.01	***
Winter.2014	Winter.2011	1.4232	2.9853	0.477	1	Ns
Winter.2013	Winter.2012	13.4669	3.2963	4.085	<0.01	**

Winter.2014	Winter.2012	-8.0329	2.5921	-3.099	0.0997	Ns
Winter.2014	Winter.2013	-21.4999	3.8093	-5.644	<0.01	***

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