Vol. 422: 93–103, 2011
doi: 10.3354/meps08925

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 31

Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future

Michael A. Rasheed[1], Richard K. F. Unsworth[2,*]

[1]Marine Ecology Group, Northern Fisheries Centre, Fisheries Queensland, Department of Employment, Economic Development and Innovation, PO Box 5396, Cairns, Queensland 4870, Australia
[2]Biological Sciences Research Unit, Glyntaf Campus, University of Glamorgan, Pontypridd CF37 1DL, UK

ABSTRACT: The long-term changes of tropical intertidal seagrass, mainly *Halodule uninervis* and *Halophila ovalis* meadows and their relationship to climate are poorly documented. Developing a greater understanding of the effects of climate on seagrass meadows is critical for estimating the effects of future climate change scenarios. Here we document the temporal dynamics of coastal intertidal seagrass in tropical northeast Australia over 16 yr of detailed monitoring. This study is the first to directly relate such change to long-term climate variability in the Indo-Pacific region and southern hemisphere. Regression modelling was used to relate seagrass biomass and meadow area measurements to climate data. The aboveground biomass and area of the meadow were correlated with the interacting factors of air temperature, precipitation, daytime tidal exposure and freshwater runoff from nearby rivers. Elevated temperature and reduced flow from rivers were significantly correlated ($R^2 = 0.6$, $p < 0.001$) with periods of lower seagrass biomass. Results of this study have important implications for the long-term viability of seagrasses with regard to climate change scenarios. Modelling of our findings indicates that future higher temperatures could be detrimental to Indo-Pacific intertidal, coastal and estuarine seagrass meadows.

KEY WORDS: Climate change · Global warming · *Halophila ovalis* · *Halodule uninervis* · Temperature · Rainfall · Indo-Pacific · Queensland · Australia

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Global climate is now undergoing a period of sustained warming (Hansen et al. 2006, IPCC 2007, Rahmstorf et al. 2007) that is predicted to continue at a rapid rate for at least the next 100 yr, resulting in temperature increases between 0.6 and 6.4°C (IPCC 2001, 2007). Existing 20th century global climate change of 0.6 ± 0.2°C has already resulted in significant ecological changes across an expanse of different ecosystems and ecological hierarchies (McCarty 2001, Walther et al. 2002, Ward et al. 2005, Hoegh-Guldberg et al. 2007, Prezeslawski et al. 2008). These responses are expected to accelerate, resulting in habitat degradation, species loss and range changes caused by increases in temperature (McCarty 2001, Poloczanska et al. 2007), storm frequency and intensity (Harley et al. 2006, Crabbe et al. 2008) and acidification of aquatic environments (Kleypas et al. 1999, Orr et al. 2005).

Almost 10% of all coastal oceans sea beds are covered by seagrass (Hemminga & Duarte 2000). While these meadows constitute only a small fraction of the global marine primary production (1.13%), they play an important role as a carbon sink (Duarte & Cebrian 1996, Kennedy & Björk 2009). Seagrass meadows also provide important ecosystem services, such as nutrient cycling (Costanza et al. 1997), providing refuge for highly productive fauna (Unsworth et al. 2008, 2010) and supporting subsistence and commercial fisheries (Watson et al. 1993, Unsworth & Cullen 2010).

Seagrass meadows are a habitat considered to be at high risk from climate change through increased thermal stress, increased storm incidence and changes in freshwater flows (Short & Neckles 1999, Waycott et al. 2007, Micheli et al. 2008); in recent times they have

*Corresponding author. Email: richardunsworth@hotmail.com

© Inter-Research 2011 · www.int-res.com

been lost at an unprecedented rate from a variety of anthropogenic influences (Waycott et al. 2009). Predictions of the influence of climate change scenarios on seagrass (Short & Neckles 1999, Harley et al. 2006, Poloczanska et al. 2007, Waycott et al. 2007) are largely based on incidences of seagrass loss associated with extreme weather (Cardoso et al. 2008, Micheli et al. 2008) as reported in short-term experimental studies (Campbell et al. 2006). Long-term studies directly measuring seagrass changes and how they are correlated with climate are rare. Such studies are restricted to the Mediterranean Sea and coastal areas of Florida (Marba & Duarte 1997, Tomasko et al. 2005); no similar studies have been reported for the tropical Indo-Pacific region.

Throughout the Indo-Pacific region, turbid estuarine and coastal environments commonly contain abundant and productive intertidal seagrass meadows dominated by the small colonising floral species of *Halodule uninervis* (Forssk.) Aschers., 1882 and *Halophila ovalis* (R.Br.) J. D. Hooker, 1858 (Lee Long et al. 1993, Coles et al. 2003). Such meadows are often spatially expansive (Lee Long et al. 1993, Coles et al. 2003) and are particularly important food sources for dugong *Dugong dugong* and green turtles *Chelonia mydas* (Bjorndal 1985, Preen & Marsh 1995). The intertidal and coastal location of these meadows makes them susceptible to large climatic events, such as flooding (Preen et al. 1995, Campbell & McKenzie 2004), drought (Cardoso et al. 2008) and elevated temperature (Campbell et al. 2006). Such meadows can be highly dynamic (Mellors et al. 1993, McKenzie 1994, Rasheed 1999), and changes in assemblage biomass and plant growth can commonly vary by up to a factor of 4 (Brouns 1985, Erftemeijer & Herman 1994, Lanyon & Marsh 1995).

It is not exactly clear how direct changes in air temperature and rainfall predicted by recent climate scenarios, and specifically those changes predicted for northern Australia (CSIRO 2007, IPCC 2007, Suppiah et al. 2007), will influence seagrass at the plant as well as at the whole meadow level within a natural environment. Air temperature has a large effect upon intertidal seagrass, both when the seagrass is exposed and when very shallow water becomes 'super-heated' because of warm air temperatures (Campbell et al. 2006). At present the responses of seagrass to variable *in situ* temperature are virtually unmeasured, especially within tropical environments (Thorhaug 1978, Agawin et al. 2001, Waycott et al. 2007). This limited knowledge of the interactions between seagrass meadows and local climatic forcing principally stems from the limited availability of long-term seagrass monitoring data linked to environmental characteristics.

The present study uses a 16 yr seagrass monitoring data set from tropical north Queensland, Australia, and analyses it in relation to available local climate data to test the following null hypotheses: (1) local climate does not correlate with seagrass meadow biomass and meadow area, and (2) proposed climate change scenarios will not affect seagrass meadows in tropical northern Australia.

MATERIALS AND METHODS

Study site. Seagrass monitored within this study was located near Karumba, a small coastal community located in the southeastern Gulf of Carpentaria, Queensland, Australia (Fig. 1). Surveys were conducted near the Port of Karumba at the mouth of the Norman River between 1994 and 2009. Sampling was conducted every October (dry season).

The coastal plain surrounding the Karumba area is typically flat with low relief rising to ~10 m above sea level. Low-density livestock grazing is the major land use for the Norman River catchment and there are no major secondary industries. Karumba has a tropical monsoon rainfall pattern with a mean annual rainfall of 889.8 mm (range, 508 to 1131 mm), of which the majority falls between December and March. Rainfall in October is rare and the maximum amount recorded between 1994 and 2009 was 5.8 mm in this month. Long-term (since 1908) mean daily minimum and maximum temperatures are 22.6 to 35.9°C in October (BOM 2010). Tidal conditions in the Gulf of Carpentaria are diurnal (Webb 1981) and their long-term cycles with respect to the hours of the day results in long-term cycles of change in the amount of exposure afforded to the intertidal area during daylight hours.

Seagrass meadow area mapping. Seagrass meadow area and biomass were measured on the shallow water mud and sand banks (known as Alligator Bank) between the Norman and Bynoe rivers covering ~1300 ha (see Fig. 1).

The boundaries of the seagrass meadow were mapped by means of GPS from aerial (helicopter) surveys conducted at low tide when the seagrass meadow was exposed. Data were digitised to a GIS basemap (McKenzie et al. 2001) with ArcGISs (Environmental Systems Research Institute). The GIS basemap was constructed from a 1:25 000 vertical aerial photograph rectified and projected to Geodetic Datum of Australia (GDA 94) coordinates. The precision of determining the seagrass meadow boundary was expressed as an estimate of reliability (R) (McKenzie et al. 2001). The reliability estimate ranged between ±10 and 15 m for the surveys and was based on the accuracy of obtaining position fixes for boundary mapping sites (McKenzie et al. 2001).

Seagrass aboveground biomass sampling. Aboveground biomass data for seagrass meadows were col-

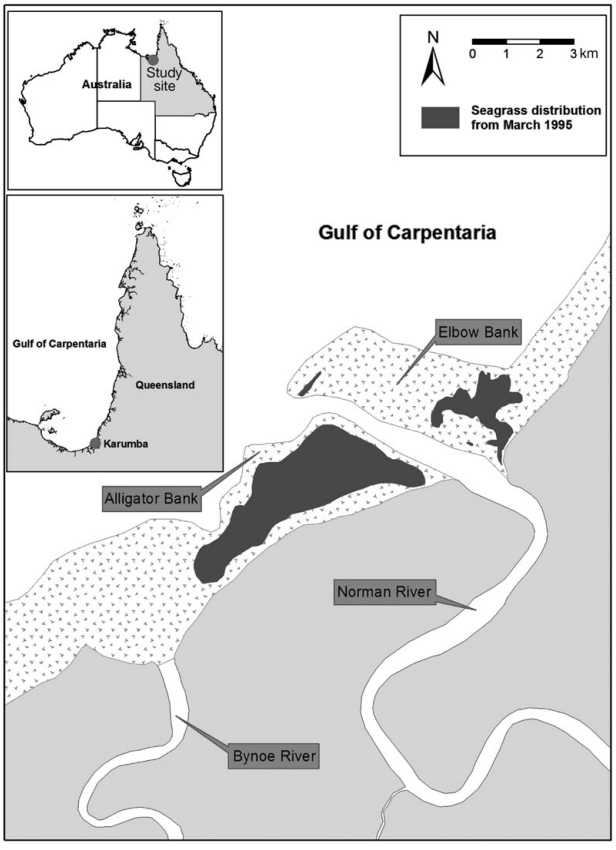

Fig. 1. Location of the seagrass meadow near the Port of Karumba, Queensland, Australia

lected at seagrass habitat characterisation sites scattered randomly within the mapped seagrass meadow. The number of sites placed within the meadow was based on the initial survey conducted in 1994 and a subsequent power analysis (Burdick & Kendrick 2001). This analysis was done to detect a 30% change in seagrass biomass between years with 90% probability and 90% statistical power according to the method described by (Bros & Cowell 1987) and was revised throughout the 16 yr of monitoring to ensure adequate sampling intensity that allowed continued detection of the desired level of change. Seagrass aboveground biomass, seagrass species composition and GPS fixes were recorded at each sampling site from a helicopter hovering within 1 m above the ground when the meadow was exposed at low tide. Seagrass species were identified according to Kuo & McComb (1989). A long-handled garden rake was also used to assist with identification of species and the accurate apportionment of species composition (i.e. by physically lifting the upper canopy to allow for the observation of smaller species potentially hidden below).

Aboveground seagrass biomass was determined at each of the sampling sites by means of a technique that visually estimates biomass as described by Mellors (1991) and is commonly used as a nondestructive method for assessing seagrass biomass change (Lee 1997, Mumby et al. 1997, Rasheed 1999, 2004, Rasheed et al. 2008, Coles et al. 2009). In Karumba, observers ranked seagrass biomass by referring to a series of 12 reference quadrat photographs that represented the range of biomass likely to be encountered (Mellors 1991, Kutser et al. 2007). The photos used were from similar seagrass habitat and assigned a reference rank ranging from 0 (no seagrass) to 5 (maximum biomass expected). This was based on the linear relationship between biomass for the photos that had been previously determined in the laboratory. Field biomass ranks were made by observers assigning a rank value (to 0.1 of a rank) by referring to the reference photos. This method was conducted on 3 random placements of a 0.25 m^2 quadrat at each site within the meadow. The relative proportion of the biomass for each seagrass species within each survey quadrat was also recorded.

At the completion of each annual survey a biomass calibration exercise was conducted. This was performed by each observer assigning a rank to a series of 6 calibration quadrats in the same manner as for the field survey. These calibration quadrats were then harvested, dried and converted into aboveground biomass in g dry weight (DW) m^{-2}. A linear regression was then calculated between the observed ranks and the measured aboveground biomass for each individual observer. Observer-specific regression equations were then applied to field ranks to convert data to aboveground biomass. The data from each individual observer was only used if the linear regression had an R^2 greater than 0.95, indicating a 95% certainty in the observers estimates, leaving a residual and quantified observer error of <5%. This technique has been successfully used to determine small changes in biomass within a range of empirical field and experimental studies (Rasheed 1999, 2004, Coles et al. 2009).

Climate data. Analysis of climate influences on seagrass meadows in Karumba focused upon the effect of 4 factors: temperature, rainfall, river flow and tidal exposure. All climate and tidal data used within this study are publically available from the Australian Bureau of Meteorology (BOM 2010) and the Queensland State Department of Environmental Resource Management (DNRMW 2010). Climate data were collected from the nearest weather station at Normanton Airport (Stn no. 029063) and the river monitoring station at Glenore Weir (Stn no. 916001B).

For each separate climate variable within each year of the 16 yr period (see Table 1), a mean value for the previous month and for 3, 6, 9 and 12 mo before seagrass monitoring was determined. This created 5 sepa-

rate variables for each individual climate factor. An index of tidal exposure was also created for the Karumba meadow. This was based on the fact that the seagrass meadow in Karumba was all of a similar depth, and that as a result the majority became exposed at the same point in time during the receding tide. Observations determined that a tidal height of <0.9 m was sufficient to uncover the entire meadow. The total daylight hours within each separate month throughout the 16 yr period that the tidal height was recorded to be less than a defined tidal height (calculated separately for heights 0.8, 0.9 and 1.0 m) was summed. For each of the 3 separate tidal heights, this was summed for the previous 1, 3, 6, 9 and 12 mo. The original 4 climate and tidal factors then created 30 separate variables for use in regression analysis.

Data analysis. Summary statistics were calculated and all mean values are displayed together with their SE values. All observations taken each year were randomly distributed and therefore considered independent observations. Data was not normally distributed and differences in mean biomass between years were therefore analysed using a 1-way Kruskal-Wallis test on ranks with SigmaPlot v. 11. Interannual comparisons were analysed by means of the Dunn's pairwise comparisons method in SigmaPlot v. 11.

To investigate which of the 30 variables correlated most with annual mean seagrass meadow biomass and area, a partial least squares (PLS) regression model was developed in Minitab (v. 15). PLS regression is an extension of multiple regression analysis in which the effects of linear combinations of several predictors on a response variable (or multiple response variables) are analysed. PLS regression is particularly suited to incidences when the matrix of predictors has more variables than observations, and when there is multicollinearity among variables (Carrascal et al. 2009). Our study had 16 observations (years) and 30 variables, and many of the variables were collinear. This technique has commonly been used to analyse a range of ecological data sets (Amand et al. 2004, Larocque et al. 2006, Carrascal et al. 2009).

All annual mean seagrass biomass data for the whole species assemblage, each annual individual species biomass and the annual total meadow area were analysed against the 30 variables. PLS regression was conducted in a step-wise manner that allowed for the successive removal of variables that did not contribute to the model, thus enabling the strongest possible PLS model to be created.

The PLS regression analysis calculated a predicted residual sum of squares (PRESS) following cross-validation. This allowed for the calculation of a predicted R^2 value in addition to a conventional R^2, hence, the determination of the predictive power of the observed relationship. A much lower predicted R^2 value than the conventional R^2 indicates the model is dependent upon only a few observations and will probably not provide a good predictive model. The model then separates the individual predictors and provides regression coefficients (analogous to correlation coefficients).

The final PLS regression models determined for the interaction between seagrass and climate (maximum 2 variables) did not contain collinear variables and the number of variables was less than the number of observations. This allowed for the use of conventional multiple linear regression to be used to develop a simple model for the prediction of future climate scenarios. These relationships were then plotted across a range of values indicative of the specific variable, including values applicable to proposed future climate scenarios for northeast Australia (CSIRO 2007, Suppiah et al. 2007).

RESULTS

Seagrasses in Karumba were confined to the shallow intertidal banks and no seagrass was found in subtidal regions. Although baseline assessments in 1995 discovered meadows on the Elbow Bank as well as the Alligator Bank (see Fig. 1), annual surveys were only conducted on the Alligator Bank. Two species of seagrass were found within the Alligator Bank monitoring meadow, *Halodule uninervis* (narrow leaf form) (Forsk.) Aschers. in Boissier, and *Halophila ovalis* (R. Br.) Hook.*f*. The meadow was dominated by *H. uninervis* and comprised low levels of *H. ovalis* (Fig. 2).

Interannual seagrass variability

The Karumba seagrass meadow had a long-term mean (±SE) biomass of 6.0 ± 0.8 g DW m^{-2} (1994 to 2009) and was significantly different between years ($H_{1,15}$ = 296, $p < 0.001$). It ranged from 0.87 g DW m^{-2} in 2002 to 13.6 g DW m^{-2} in 2006 (Fig. 2a). The first 8 yr of monitoring were characterised by intermediate biomass of low variability, but in 2002 biomass was reduced for 2 yr (Fig 2a). The period of highest biomass, 2006 to 2009, also had the highest interannual variability. Interannual variability was more pronounced for the *Halodule uninervis* component of the assemblage than for the lower biomass *Halophila ovalis*. *H. uninervis* had a long-term mean (±SE) biomass of 5.4 ± 0.8 g DW m^{-2}, which ranged from 0.75 g DW m^{-2} in 2002 to 13.2 g DW m^{-2} in 2006 (Fig. 2a). *H. ovalis* had a long-term mean (±SE) biomass of 0.6 ± 0.1 g DW m^{-2} that ranged from a minimum of 0.1 g DW m^{-2} in 2002 to a maximum of 1.9 g DW m^{-2} in 1998 (Fig. 2a).

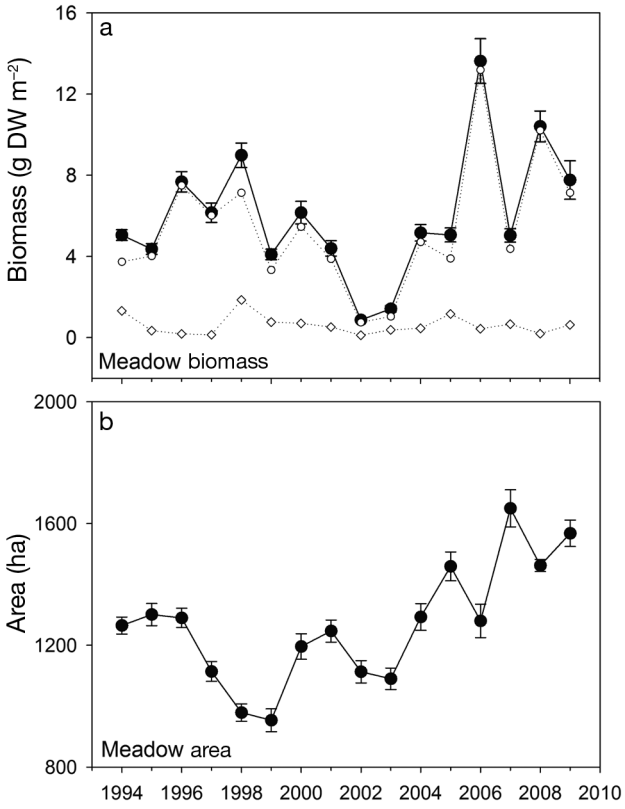

Fig. 2. *Halodule uninervis* and *Halophila ovalis*. Mean (±SE) annual habitat parameters, (a) meadow biomass and (b) meadow area, recorded each October between 1994 and 2009 for an intertidal seagrass in Karumba. ●: total seagrass biomass, ○: *H. uninervis* biomass and ◇: *H. ovalis* biomass

Seagrass meadow area averaged (± estimate of reliability) 1266 ± 49 ha. This ranged from 954 ha in 1999 to 1649 ha in 2007 (Fig. 2b). After commencement of monitoring in 1994 an initial general trend of declining area occurred until 1999, when the seagrass meadow area reached its minimum. Seagrass meadow area since 1999 has been generally increasing with >1400 ha found in 4 of the 5 yr up to 2009 (Fig. 2b). Seagrass was also monitored in Karumba during the wet season (March) from 1994 to 2000. Data is not presented here in detail as the number of data points were considered insufficient for a correlative analysis. Seagrass biomass was generally higher, but more variable, in March relative to October. Mean (±SE) October biomass (1994 to 2000) was 6.2 ± 0.4 g DW m^{-2} and mean March biomass was 9.5 ± 0.7 g DW m^{-2}.

Climate conditions

During this 16 yr period, there was interannual climate variability observed in temperature (mean October temperature, 36.0 ± 0.4°C) and rainfall (mean October rainfall, 11.2 ± 4.1 mm). Mean annual daily maximum temperature was variable throughout the 16 yr of monitoring, ranging from a mean of 32.0 mm in 2003 to a mean of 34.1 mm in 2006. Annual rainfall was also highly varied throughout the 16 yr with a mean (±SE) annual total of 881 ± 81 mm. The periods 1994 to 1996 and 2002 to 2005 were characterised by low rainfall (Fig. 3). These periods resulted in reduced flow of the Norman River (Fig. 3). Flow reached a low for the total of the previous 12 mo of 10 gigalitres (Gl) in 2005 and a maximum of 650 Gl in October 1998 (Fig. 3). The number of daily daylight hours of tidal exposure also varied highly between years as a result of long-term lunar cycles. Mean (±SE) number of annual daylight hours of exposure was 338 ± 30 h, ranging from 132 in 1999 to 567 in 2007.

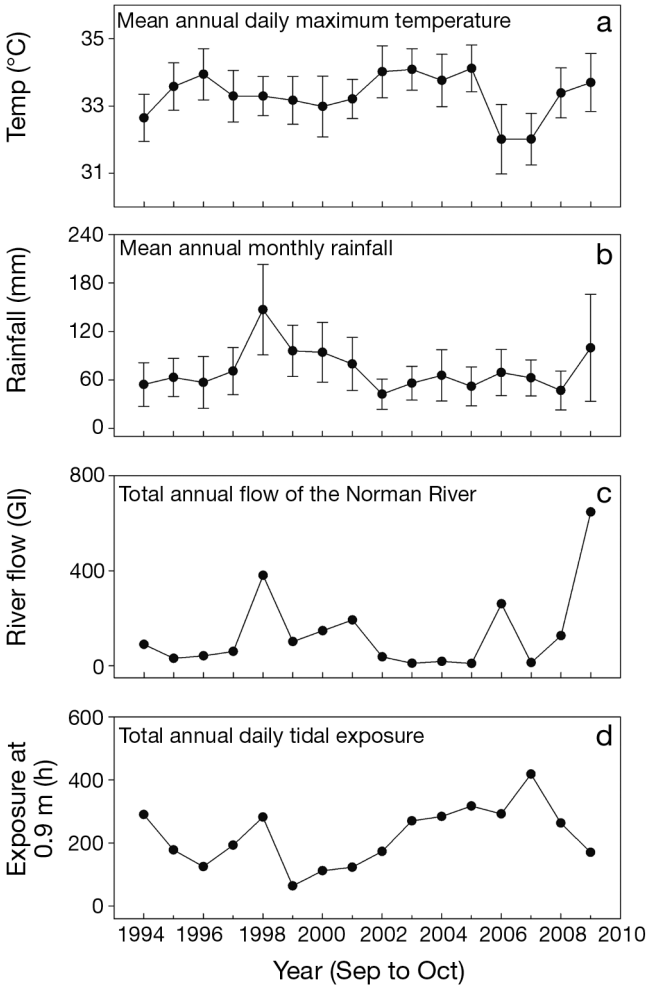

Fig. 3. Mean (±SE) annual (a) daily maximum air temperature (Temp), and (b) monthly rainfall. (c) Total annual river flow and (d) total daytime hours that the seagrass meadow was subjected to a tidal height <0.9 m in Karumba between 1994 and 2009 (Normanton weather station)

Climate and seagrass relationships

Examination of the relationship between climate factors (including averages for each previous month interval (e.g. 1, 3, 6, 9 and 12 mo) with mean seagrass biomass and meadow area values revealed that river flow, rainfall, air temperature and tidal exposure were all correlates of seagrass in Karumba (Table 1).

The initial PLS regression models containing all the environmental predictor variables demonstrated that many of the variables were not good predictors for the variance of the Karumba meadow (in terms of total seagrass biomass, species biomass and meadow area). Stepwise removal of successive predictor variables that did not contribute to the models enhanced the ability of the predictors (environmental data) to explain the interannual variability (biomass and area).

The variance of the biomass of the whole seagrass assemblage was significantly correlated to air temperature (previous 3 mo) and river flow (previous 9 mo) ($F_{2,15}$ = 10.4, p < 0.001). The whole model explained 61% of the variance of the seagrass biomass (R^2 = 0.61). More than 99% of the explained (i.e. of the 61%) variance in the model was within its first component. Following cross-validation, the model for seagrass assemblage biomass still explained 21% of the variation (predicted R^2 = 0.21). When the model was broken down to regression coefficients, seagrass biomass was negatively correlated with air temperature for the previous 3 mo (coefficient = –0.62) and positively correlated with river flow for the previous 9 mo (coefficient = 0.56) (Table 1). The model for *Halodule uninervis* biomass was very similar to the model for overall assemblage biomass but had an improved predicted R^2 of 0.35.

The model for *Halophila ovalis* was based upon a significant positive correlation ($F_{1,15}$ = 16.7, p < 0.001) with the total previous 12 mo rainfall (Table 1). The model for *H. ovalis* biomass explained 56% of the interannual variance (R^2 = 0.56). Following cross-validation, the model for *H. ovalis* biomass still explained 27% of the variation (predicted R^2 = 0.27).

Seagrass meadow area was significantly and positively correlated with tidal exposure (previous 6 mo). The model for seagrass meadow area, although significant ($F_{1,15}$ = 5.5, p < 0.05) only explained 28% of the interannual variance (R^2 = 0.28). Following cross-validation, the model for seagrass meadow area explained 5% of the variation (predicted R^2 = 0.05).

Modelling future climate

A model was created to determine the effect of future climatic predictions proposed for north Queensland (CSIRO 2007, Suppiah et al. 2007) on overall seagrass assemblage biomass. This model used the predictor correlates of seagrass biomass determined

Table 1. Partial least squares (PLS) regression analysis (final models following stepwise analysis) of annual mean seagrass biomass and meadow area relative to available climate and environmental data at Karumba, north Queensland, Australia (1994 to 2009). Table shows the overall 'global' ANOVA statistics for each of the regression models, the individual principal components and their cumulative R^2 values. Table also shows the values computed by the PLS model of the variance explained with the *x*-axis (*x*-var.). Individual regression coefficients of the specific biomass predictors (with time series considered in brackets) are also shown. Exp. = exposure, Temp. = air temperature

Metric		PLS ANOVA			Model selection and validation				Biomass predictors			
		p	*F*	df	Component	*x*-var.	R^2	R^2 (pred)	Tidal exp. (6 mo)	Temp. (3 mo)	River flow (9 mo)	Rainfall (12 mo)
All seagrass biomass	ANOVA	<0.001	10.4	2,15								
	PLS Model				1	0.43	0.61	0.19				
					2	1.0	0.61	0.21				
	Coefficients									–0.62	0.56	
Halodule uninervis biomass	ANOVA	<0.001	9.9	2,15								
	PLS Model				1	0.43	0.60	0.23				
					2	1.0	0.61	0.35				
	Coefficients									–0.64	0.52	
Halophila ovalis biomass	ANOVA	<0.001	16.7	1,15								
	PLS Model				1	1.0	0.56	0.27				
	Coefficients											0.75
Seagrass meadow area	ANOVA	<0.05	5.5	1,15								
	PLS Model				1	1.0	0.28	0.05	0.53			
	Coefficients											

within the final PLS analysis and reanalysed them with multiple regression to determine an equation for extrapolation. Multiple regression was determined to be applicable as final predictor variables were retested for collinearity. River flow over the previous 9 mo and temperature over the previous 3 mo were not collinear and data were therefore used in a multiple regression. The following equation was calculated for seagrass biomass (B), where r = river flow and t = temperature:

$$B = 73.7 + 0.000001r - 2.18t \quad (1)$$

The proposed climate predictions were then extrapolated onto these equations to hypothesise what might happen to seagrass biomass based on such scenarios. Based upon a model of the relationship between seagrass biomass, air temperature and river flow (1994 and 2009), we propose that if average maximum daily temperature rises by 0.5°C (the minimum proposed range for 2030) seagrass biomass in Karumba may be reduced by 21%. By 2030, the temperature could potentially rise by 1.4°C; this would potentially result in a complete loss of intertidal seagrass at Karumba. By 2070 we propose this reduction could be between 53 and 100% (Table 2, Fig. 4). The proposed future rainfall (as river flow) scenarios were modelled and found unlikely to result in large changes in seagrass biomass.

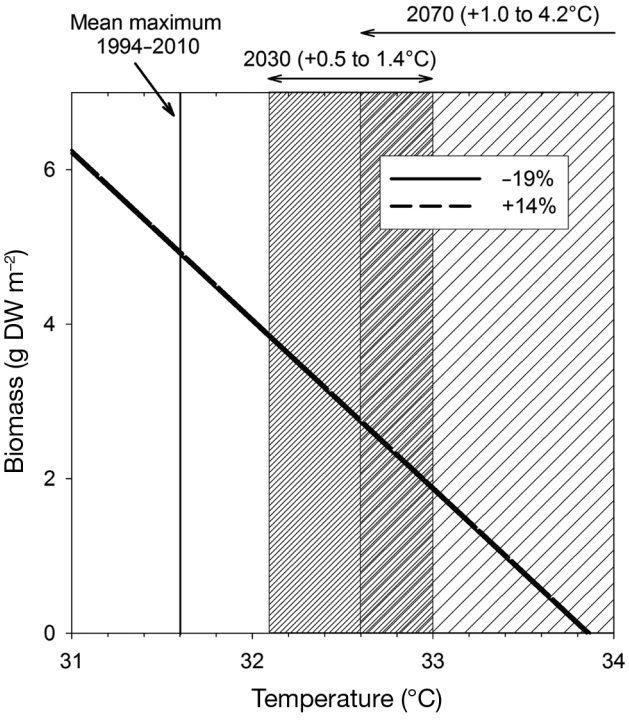

Fig. 4. Proposed model of the relationships between intertidal seagrass meadow biomass, river flow and air temperature. Equations were derived from multiple regression modelling of seagrass habitats from Karumba between 1994 and 2009. The model is calculated for 2 river-flow scenarios (–19 and +14%) based upon estimations determined for rainfall for north Queensland between 2010 and 2070 (CSIRO 2007, Suppiah et al. 2007) and plotted against a range of temperatures. Values for the range of future rainfall scenarios (+14 to –19%) do not have significant major effect upon seagrass biomass as can be seen by their convergence into 1 line. Superimposed on this model are the ranges of temperature (shaded bands) expected for north Queensland in 2030 and 2070 (CSIRO 2007, Suppiah et al. 2007)

DISCUSSION

This study is the first detailed long-term study of a tropical seagrass meadow in relation to multiple aspects of local climate in the tropical Indo-Pacific region or southern hemisphere. Seagrass biomass and distribution in a turbid intertidal environment was highly variable throughout a 16 yr period (1994 to 2009). This variability was correlated with climate (river flow and temperature) and long-term tidal exposure cycles. Recent evidence has confirmed that seagrass meadows are one of the most productive shallow water ecosystems (Margalef 1986, Stevenson 1988, Duarte & Cebrian 1996, Duarte & Chiscano 1999, Rasheed et al. 2008). These findings present concern given the expected future climate scenarios of increased temperatures and more variable rainfall.

Seagrass community biomass (and *Halodule univervis* biomass in particular) was highly correlated with an interaction between air temperatures and river flow. River flow was a positive correlate and air temperature a negative correlate with biomass. The biomass of the small colonising species *Halophila ovalis*, which was a minor assemblage component, was positively correlated with rainfall; temperature was not a correlate with *H. ovalis*. Although incidences of high short-term rainfall and flooding have commonly resulted in detrimen-

Table 2. *Halodule uninervis* and *Halophila ovalis*. Percentage reduction in seagrass biomass under climate conditions proposed for northern Queensland in 2030 and 2070 (Suppiah et al. 2007) calculated using the relationship between meadow seagrass biomass, river flow and air temperature. Equation derived from multiple regression modelling of seagrass habitats from Karumba, north Queensland, between 1994 and 2009 with environmental data

Year	Temperature increase (°C)	Proposed rainfall change (%) 2030		2070	
		–6	5	–19	14
2030	+0.5	21	21		
	+1.4	100	100		
2070	+1.0			54	53
	+4.2			100	100

tal effects on seagrass meadows (Campbell & McKenzie 2004, Cardoso et al. 2008), terrestrial water flows are important in supplying nutrients into coastal seagrass meadows (Short 1987, Udy et al. 1999). Therefore, these findings are similar to those for temperate seagrasses (Marba & Duarte 1997) and suggest that the periods of drought that were experienced between 2002 and 2006, when the Norman River almost completely stopped flowing, may have been detrimental by not supplying sufficient nutrients to seagrass meadows. Alternative explanations for the positive effect of river flow could also relate to the effect of salinity on the germination of seeds (Orth et al. 2000). Although we document the major correlates of seagrass in the dry season, seagrass biomass was recorded to be higher in the wet season. Therefore, it is important to recognise that the factors influencing seagrass may alter between these seasons as environmental factors and growth dynamics are different between seasons.

Seagrasses are widely known to be sensitive to elevated temperature, with both laboratory and field data indicating that tropical seagrasses undergo thermally induced physiological stress at temperatures >35°C (Bulthuis 1983, Ralph 1998, Campbell et al. 2006). Specifically *Halodule uninervis* has reduced photosynthetic efficiency at 35°C (Campbell et al. 2006). Temperature stress can result not just from seagrass being subjected to elevated seawater temperatures, but additionally, intertidal seagrass can be subjected to desiccation stress during periods of low tide during daylight hours (Dawson & Dennison 1996, Stapel 1997, Durako & Kunzelman 2002). Shallow water temperature can also fluctuate highly depending upon the air temperature. We found that during periods where the average air temperature exceeded 32°C, seagrass biomass was at its lowest. Average maximum daily air temperatures of 32°C are likely to have resulted in absolute *in situ* monthly maximum temperatures possibly exceeding 35°C (in the sun rather than in the shade, as air temperature is recorded under shade). Such temperatures would result in the 'super-heating' of shallow pooling water at low or reduced tidal height. Temperatures in excess of 40°C have commonly been observed in similar *H. uninervis* dominated seagrass meadows throughout Queensland due to 'super-heating' with resultant 'burning' of seagrass (McKenzie & Unsworth 2009).

Total seagrass meadow area was observed to have a weak positive correlation with the number of hours of daylight tidal exposure. This was in contrast to the correlation of biomass to temperature and river flow. It is not unexpected that a range of different factors influence seagrass change. The investment in aboveground biomass is not necessarily directly related to spatial cover, as a large meadow could have a high or low biomass, and the area could have expanded whilst the biomass declined (or vice versa) and reflects how the plant (or plants) has invested its resources. The result of a positive correlation between area and daylight tidal exposure is, however, unexpected given the potential for such periods to result in heat, desiccation and UV stress (Björk et al. 1999, Campbell et al. 2006) and is in contrast to results of analysis of an *Enhalus acoroides* meadow, also located in north Queensland (Chartrand & Rasheed 2009). In contrast to the large-leaved *E. acoroides*, *Halodule uninervis* at Karumba is narrow and small leaved, enabling leaves to potentially lie flat on wet sediment and avoid some of the desiccation risk. The positive correlation to tidal exposure probably relates to the low light environment of this turbid coastal estuarine environment. The expansion of the seagrass meadow area may result from new growth of the rhizomes together with increased reproductive effort and success. Studies on the Caribbean tropical seagrass *Thalassia testudinium* have found that belowground biomass and growth is correlated with underwater irradiance, daylength and temperature (Kaldy & Dunton 2000). Light availability is a primary controlling factor of seagrass physiology and resultant productivity (Ralph et al. 2007). Seagrasses living in low-light turbid conditions, such as found at Karumba, may be at (or near) their photosynthetic compensation point (Falkowski & Raven 1997). A reduction in the light regime below this point may result in seagrasses showing sublethal effects such as a cessation of processes of growth and cell maintenance. Because seagrass meadows in Karumba are already in a naturally turbid low-light environment (hence their restricted distribution to the intertidal zone) any further reduction in light associated with reduced tidal exposure is likely to result in reduced productivity of Karumba seagrass meadows.

The models created here, although significant, left large levels of unexplained variability (e.g. 39% for the temperature and river flow versus biomass model). These findings indicate that the climatic and environmental factors measured in the present study are not the only important correlates of seagrass change. Although sampling error could be a minor component of this unexplained variability, biological and physical factors, such as herbivory and disturbance, as well as other climatic variables, such as high wind from a specific direction, could also influence seagrass biomass. Throughout the 16 yr of surveys, dugong feeding trails were commonly observed within these seagrass meadows and could be a factor in determining seagrass community dynamics, as has been observed elsewhere on the coast of Australia (Aragones et al. 2006). Such factors may further explain some of the remaining variability within our data sets.

Future climate scenarios applied to the present models predict that by 2030 seagrass biomass in Karumba could be reduced by a minimum of 21%. If current rates of climate change continue, by 2070 we propose this reduction could be between 53 and 100%. Proposed scenarios of changing rainfall are unlikely to have a large influence on seagrass biomass. This is because such proposed changes (+19 to −14%) are small relative to the high natural interannual variability largely driven by major storm events and cyclones.

It is important to recognise that these predictions are purely based on extrapolation. Predictions beyond observed conditions assume that relationships observed over the 16 yr between temperature, river flow and seagrass biomass will continue to be linear. This relationship could become a logarithmic decline in biomass as conditions reach a critical environmental level, or alternatively, seagrass may reach a low asymptotic level of biomass as conditions allow for short bursts of colonising flora to persist.

In conclusion, we present a novel study relating seagrass biomass to long-term climatic changes and find the high variability of a coastal intertidal seagrass meadow throughout a 16 yr period to be correlated with river flow and air temperature. This study has important implications for the future viability of intertidal seagrass meadows in the tropics, as many studies have inferred that some seagrass species under certain climate change scenarios could benefit from being released from carbon limitation (Palacios & Zimmerman 2007, Hall-Spencer et al. 2008). Although this is a highly likely consequence of climate change for many seagrass species and meadows, the findings of our study support those of recent investigations (Campbell & McKenzie 2004, Campbell et al. 2006, Waycott et al. 2007, Cardoso et al. 2008) to illustrate that future climate scenarios of higher air temperatures could also be highly detrimental to coastal and estuarine intertidal seagrass meadows.

Acknowledgements. This paper represents an analysis of results made possible only by the hard work of numerous individuals throughout 16 yr. The authors therefore thank the following: W. Baker, R. Coles, P. Daniel, K. Dew, B. Foster, D. Foster, S. Hollywood, L. Johns, W. Lee-Long, L. Makey, S. McKenna, L. McKenzie, C. Roder, A. Roelofs, T. Sankey, H. Taylor and R. Thomas. The authors also acknowledge the financial support of the Ports Corporation of Queensland Ltd., Queensland, Fisheries Queensland, and the CRC Reef Research Centre. Thanks also to S. De Grave and B. Mayer for providing expert statistical advice.

LITERATURE CITED

Agawin N, Duarte CM, Fortes MD, Uri J, Vermaat J (2001) Temporal changes in the abundance, leaf growth and photosynthesis of three co-occurring Philippine seagrasses. J Exp Mar Biol Ecol 260:217–239

Amand M, Pelletier D, Ferrari J, Kulbicki M (2004) A step toward the definition of ecological indicators of the impact of fishing on the fish assemblage of the Abore reef reserve (New Caledonia). Aquat Living Resour 17:139–149

Aragones LV, Lawler IR, Foley WJ, Marsh H (2006) Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? Oecologia 149:635–647

Björk M, Uka J, Weil A, Beer S (1999) Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Mar Ecol Prog Ser 191:121–126

Bjorndal KA (1985) Nutritional ecology of sea turtles. Copeia 1985:736–751

BOM (Bureau of Meteorology) (2010) Australian Federal Bureau of Meteorology weather records. Available at: www.bomgov.au

Bros WE, Cowell BC (1987) A technique for optimising sample size (replication). J Exp Mar Biol Ecol 114:63–71

Brouns JJWM (1985) A comparison of the annual production and biomass in three monospecific stands of the eelgrass *Thalassia hemprichii* (Ehrenb.) Aschers. Aquat Bot 23: 149–175

Bulthuis DA (1983) Effects of temperature on the photosynthesis–irradiance curve of the Australian seagrass, *Heterozostera tasmanica.* Mar Biol Lett 4:47–57

Burdick DM, Kendrick GA (2001) Standards for seagrass collection, identification and sample design. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier Science, Amsterdam, p 82–100

Campbell SJ, McKenzie LJ (2004) Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. Estuar Coast Shelf Sci 60:477–490

Campbell SJ, McKenzie LJ, Kerville SP (2006) Photosynthetic responses of seven tropical seagrasses to elevated seawater temperature. J Exp Mar Biol Ecol 330:455–468

Cardoso PG, Raffaelli D, Pardal MA (2008) The impact of extreme weather events on the seagrass *Zostera noltii* and related *Hydrobia ulvae* population. Mar Pollut Bull 56: 483–492

Carrascal LM, Galvan I, Gordo O (2009) Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118:681–690

Chartrand KM, Rasheed MA (2009) Port of Weipa long term seagrass monitoring, 2000–2008. DPI&F Publication PR09-4201. Queensland Government, Department of Primary Industries and Fisheries, Cairns

Coles RG, McKenzie LJ, Campbell SJ (2003) The seagrasses of eastern Australia. In: Green EP, Short FT (eds) World atlas of seagrasses. University of California Press, Berkeley, CA

Coles R, McKenzie L, De'ath G, Roelofs A, Long WL (2009) Spatial distribution of deepwater seagrass in the inter-reef lagoon of the Great Barrier Reef World Heritage Area. Mar Ecol Prog Ser 392:57–68

Costanza R, d'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Crabbe MJC, Martinez E, Garcia C, Chub J, Castro L, Guy J (2008) Growth modelling indicates hurricanes and severe storms are linked to low coral recruitment in the Caribbean. Mar Environ Res 65:364–368

CSIRO (Commenwealth Scientific and Industrial Research Organisation) (2007) Climate change in Australia. CSIRO and the Australian Bureau of Meterology Joint Report. Available at: www.climatechangeinaustralia.gov.au/resources.php

Dawson SP, Dennison WC (1996) Effects of ultraviolet and photosynthetically active radiation on five seagrass species. Mar Biol 125:629–638

DNRMW (Department of Natural Resources, Mines and Water) (2010) Queensland State Department of Natural Resources, Mines and Water. Available at: www.nrw.qld.gov.au/

Duarte CM, Cebrian J (1996) The fate of autotrophic production in the sea. Limnol Oceanogr 41:1758–1766

Duarte CM, Chiscano CL (1999) Seagrass biomass and production: a reassessment. Aquat Bot 65:159–174

Durako MJ, Kunzelman JI (2002) Photosynthetic characteristics of *Thalassia testudinum* measured *in situ* by pulse-amplitude modulated (PAM) fluorometry: methodological and scale-based considerations. Aquat Bot 73:173–185

Erftemeijer PLA, Herman PMJ (1994) Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99:45–59

Falkowski PG, Raven JA (1997) Aquatic photosynthesis. Blackwell Science, Malden, MA

Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E and others (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454:96–99

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. Proc Natl Acad Sci USA 103:14288–14293

Harley CDG, Hughes AR, Hultgren KM, Miner BJ and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS and others (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

IPCC (Intergovernmental Panel on Climate Change) (ed) (2001) Climate 2001: synthesis report. A contribution of working groups I, II, and III to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

IPCC (2007) Climate change 2007: the physical science basis. Summary for policymakers. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. IPPC, Geneva

Kaldy JE, Dunton KH (2000) Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. Mar Ecol Prog Ser 193:271–283

Kennedy K, Björk M (2009) Seagrass meadows. In: Laffoley Dd'A, Grimsditch G (eds) The management of natural coastal carbon sinks. IUCN, Gland, p 23–29

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284:118–120

Kuo J, McComb AJ (1989) Seagrass taxonomy, structure and development. In: Larkum AWD, McComb AJ, Sheperd SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, New York, NY, p 6–73

Kutser T, Vahtmäe E, Roelfsema CM, Metsamaa L (2007) Photo-library method for mapping seagrass biomass. Estuar Coast Shelf Sci 75:559–563

Lanyon JM, Marsh H (1995) Temporal changes in the abundance of some tropical intertidal seagrasses in North Queensland. Aquat Bot 49:217–237

Larocque I, Pienitz R, Rolland N (2006) Factors influencing the distribution of chironomids in lakes distributed along a latitudinal gradient in northwestern Quebec, Canada. Can J Fish Aquat Sci 63:1286–1297

Lee SY (1997) Annual cycle of biomass of a threatened population of the intertidal seagrass *Zostera japonica* in Hong Kong. Mar Biol 129:183–193

Lee Long WJ, Mellors JE, Coles RG (1993) Seagrasses between Cape York and Hervey Bay, Queensland, Australia. Aust J Mar Freshw Res 44:19–32

Marba N, Duarte CM (1997) Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral zone. Limnol Oceanogr 42:800–810

Margalef R (1986) Ecologia. Ediciones Omega, Barcelona

McCarty JP (2001) Ecological consequences of recent climate change. Conserv Biol 15:320–331

McKenzie LJ (1994) Seasonal changes in biomass and shoot characteristics of a *Zostera capricorn* Aschers. dominant meadow in Cairns Harbour, northern Queensland. Mar Freshw Res 45:1337–1352

McKenzie LJ, Unsworth RKF (2009) Great Barrier Reef water quality protection plan (Reef Rescue) — marine monitoring program: intertidal seagrass. Final report for the sampling period 1 September 2008–31 May 2009. Fisheries Queensland, Cairns

McKenzie LJ, Finkbeiner MA, Kirkman H (2001) Methods for mapping seagrass distribution. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier Science, Amsterdam, p 101–121

Mellors JE (1991) An evaluation of a rapid visual technique for estimating seagrass biomass. Aquat Bot 42:67–73

Mellors JE, Marsh H, Coles RG (1993) Intra-annual changes in seagrass standing crop, Green Island, northern Queensland. Mar Freshw Res 44:33–42

Micheli F, Bishop MJ, Peterson CH, Rivera J (2008) Alteration of seagrass species composition and function over two decades. Ecol Monogr 78:225–244

Mumby PJ, Edwards AJ, Green EP, Anderson CW, Ellis AC, Clark CD (1997) A visual assessment technique for estimating seagrass standing crop. Aquat Conserv: Mar Freshw Ecosyst 7:239–251

Orr JC, Fabry VJ, Aumont O, Bopp L and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Orth RJ, Harwell AC, Bailey EM, Bartholomew A and others (2000) A review of issues in seagrass seed dormancy and germination: implications for conservation and restoration. Mar Ecol Prog Ser 200:277–288

Palacios SL, Zimmerman RC (2007) Response of eelgrass *Zostera marina* to CO_2 enrichment: possible impacts of climate change and potential for remediation of coastal habitats. Mar Ecol Prog Ser 344:1–13

Poloczanska ES, Babcock RC, Butler A, Hobday AJ and others (2007) Climate change and Australian marine life. Oceanogr Mar Biol Annu Rev 45:407–478

Preen A, Marsh H (1995) Response of dugongs to large-scale loss of seagrasses in Hervey Bay. Aust Wildl Res 22: 507–519

Preen AR, Lee Long WJ, Coles RG (1995) Flood and cyclone related loss, and partial recovery, of more than 1,000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquat Bot 52:3–17

Prezeslawski R, Ahyong S, Bryne M, Worheides G (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. Glob Change Biol 14:2773–2795

Rahmstorf S, Cazenave A, Church JA, Hansen JE, Keeling RF, Parker DE, Somerville RCJ (2007) Recent climate observations compared to projections. Science 316:709

Ralph PJ (1998) Photosynthetic response of laboratory-cultured *Halophila ovalis* to thermal stress. Mar Ecol Prog Ser 171:123–130

Ralph PJ, Durako MJ, Enriquez S, Collier CJ, Doblin MA (2007) Impact of light limitation on seagrasses. J Exp Mar Biol Ecol 350:176–193

Rasheed MA (1999) Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland Australia. J Exp Mar Biol Ecol 235: 183–200

Rasheed MA (2004) Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. J Exp Mar Biol Ecol 310:13–45

Rasheed MA, Dew KR, McKenzie LJ, Coles RG, Kerville S, Campbell SJ (2008) Productivity, carbon assimilation and intra-annual change in tropical reef platform seagrass communities of the Torres Strait, north-eastern Australia. Cont Shelf Res 28:2292–2303

Short FT (1987) Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. Aquat Bot 27:41–57

Short FT, Neckles HA (1999) The effects of global climate change on seagrasses. Aquat Bot 63:169–196

Stapel J (1997) Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. Mar Ecol Prog Ser 148:251–262

Stevenson JC (1988) Comparitive ecology of submersed grass beds in freshwater, estuarine and marine environments. Limnol Oceanogr 33:867–893

Suppiah R, Macadam I, Whetton PH (2007) Climate change projections for the tropical rainforest region of North Queensland. CSIRO report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns

Thorhaug A (1978) The effect of heated effluents from power plants on seagrass (*Thalassia*) communities quantitatively comparing estuaries in the subtropics to the tropics. Mar Pollut Bull 9:181–187

Tomasko DA, Corbett CA, Greening HS, Raulerson GE (2005) Spatial and temporal variation in seagrass coverage in Southwest Florida: assessing the relative effects of anthropogenic nutrient load reductions and rainfall in four contiguous estuaries. Mar Pollut Bull 50:797–805

Udy JW, Dennison WC, Lee Long WJ, McKenzie LJ (1999) Responses of seagrass to nutrients in the Great Barrier Reef, Australia. Mar Ecol Prog Ser 185:257–271

Unsworth RKF, Cullen LC (2010) Recognising the necessity for Indo-Pacific seagrass conservation. Conserv Lett 3: 63–73

Unsworth RKF, De Leon PS, Garrard SL, Jompa J, Smith DJ, Bell JJ (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. Mar Ecol Prog Ser 353:213–224

Unsworth RKF, De Grave S, Goulding L (2010) Influence of environmental cycles upon tropical seagrass caridean shrimp. Raffles Bull Zool 58:177–183

Walther GR, Post E, Convey E, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Ward DH, Reed A, Sedinger JS, Blacks JM, Derkesen DV, Castelli PM (2005) North American Brant: effects of changes in habitat and climate on population dynamics. Glob Change Biol 11:869–880

Watson RA, Coles RG, Lee Long WJ (1993) Simulation estimates of annual yield and landed value for commercial penaeid prawns from a tropical seagrass habitat, northern Queensland, Australia. Mar Freshw Res 44:211–220

Waycott M, Collier C, McMahon K, Ralph PJ, McKenzie LJ, Udy JW, Grech A (2007) Vulnerability of seagrasses in the Great Barrier Reef to climate change. In: Johnson JE, Marshall PA (eds) Climate change and the Great Barrier Reef: a vulnerability assessment. Great Barrier Reef Marine Park Authority, Townsville, p 193–236

Waycott M, Duarte CM, Carruthers TJB, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Webb DJ (1981) Numerical modal of the tides in the Gulf of Carpentaria and the Arafura Sea. Mar Freshw Res 32: 31–44

Editorial responsibility: Just Cebrian, Dauphin Island, Alabama, USA

Submitted: June 29, 2009; Accepted: November 8, 2010
Proofs received from author(s): January 15, 2011