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Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia.

Michael A. Rasheed[a*], Skye A. McKenna[a], Alexandra Carter[a], and Robert G. Coles[a]

[a] James Cook University, Centre for Tropical Water & Aquatic Ecosystem Research, PO Box 6811, Cairns QLD 4870, Australia.

[*] Corresponding author: michael.rasheed@jcu.edu.au; Telephone: +61 7 42322010

skye.mckenna@jcu.edu.au; alexandra.carter@jcu.edu.au; rob.coles@jcu.edu.au

Highlights

- Major storms and climate events resulted in large scale losses of tropical seagrasses.
- Recovery varied between meadows and species with many failing to re-establish.
- Deep water seagrass species re-colonised but shallow species failed to recover.
- The variable presence of seed banks was the main cause of differences in seagrass recovery.
- Meadows relying on clonal growth were highly vulnerable to large scale impacts.

ABSTRACT

Tropical seagrass decline and recovery from severe storm impacts was assessed via quarterly measurements of seagrass biomass, species composition and experimental investigations of recovery in north Queensland. Shallow and deep seagrass meadows suffered major declines. Significant recovery in the two years following loss only occurred at deeper sites. *Halophila* spp. in deep water areas had a high capacity for recovery through the availability of seed banks. In contrast, the shallow species did not recover quickly from experimental disturbance, had poor seed reserves and relied on asexual propagation. The potential for shallow species to recover rapidly from widespread losses was limited as seed banks were limited or non-existent. Understanding inter- and intra-specific differences in seagrass recovery and how this interacts with location is critical to predict the consequences of climate events to tropical seagrasses. This is especially important as more frequent severe storms are predicted as a consequence of climate change.

Keywords

Seagrass; loss; recovery; climate; seed; reproduction

Introduction

In recent years wide spread loss of seagrass meadows in the Great Barrier Reef (GBR) caused by weather and climate events have emphasized the need to understand the processes and timing of seagrass recovery (McKenzie et al., 2012). The frequency and severity of storms and climate conditions, including multiple above-average wet seasons in the tropics is, likely to increase as a consequence of climate change (Harley et al. 2006, Crabbe et al. 2008). This has the potential to substantially impact GBR seagrasses and reduce their capacity for recovery. The mechanisms for climate events to cause seagrass loss are relatively well documented (e.g. Campbell and McKenzie, 2004; Preen and Marsh, 1995; Ralph et al., 2007), but the capacity and mechanisms for recovery are poorly understood.

In the southern hemisphere summer of 2010/2011 Queensland, Australia experienced a series of extreme weather events driven by a La Niña weather system. This La Niña system was one of the strongest on record and caused high and prolonged rainfall and flooding. Nearly all rivers within the GBR region produced record flows (Devlin et al., 2012). Major flood plumes were observed across ~39% of the GBR marine park (Devlin et al., 2012). The La Niña also triggered three severe tropical storms that directly affected the north Queensland coast over the summer of 2010/2011: Tropical Cyclone (TC) Tasha (December 2010), TC Anthony (January 2011) and TC Yasi (February 2011). TC Yasi was the first category five cyclone (the most severe category possible) to cross the Queensland coast since 1918. Approximately 98% of intertidal seagrass area was lost in the regions directly affected by TC Yasi's path, and only a few isolated shoots remained in many coastal and reef habitats where long term seagrass cover assessments were conducted (McKenzie et al., 2012).

Queensland's coastal habitats are regularly exposed to flooding and cyclones, but the scale and longevity of the 2010/11 La Niña events were unprecedented. Three of the four summers between 2007 and 2011 in Queensland have had above average rainfall associated with La Niña conditions. Storms and cyclones have the potential to negatively impact seagrass either physically via burial, scouring and direct removal of plants and seed banks (Bach et al., 1998; Campbell and McKenzie, 2004; Preen and Marsh, 1995) or physiologically via light limitation, excess nutrients and low salinity (Bjork et al., 1999; Chartrand et al., 2012; Ralph et al., 2007). Large scale mortality of seagrasses associated with low salinity and higher water temperature caused by flood conditions have previously been documented (McKenzie et al., 2010; Waycott et al., 2005). Tropical Queensland seagrasses have a capacity to recover from climate-associated disturbance, returning to pre-impact levels within 4 months to 60 months (Campbell and McKenzie, 2004; McKenzie et al., 2003; McKenzie et al., 2012; Rasheed, 1999; Rasheed, 2004) although full recovery of some meadows may take longer than 10 years in some instances (Birch & Birch 1984). The mechanisms for recovery and the variability in timing, however, are often unclear.

Studies have shown a high reliance on asexual colonisation and clonal growth for recovery of many tropical seagrass meadows including experimental investigations in Queensland (Rasheed, 1999; 2004) and examination of small scale disturbances in Florida and the Philippines (Kenworthy et al., 2002; Rollon et al., 1999). However seed banks and seed recruitment are also likely to have a major role in the recovery process, particularly when widespread seagrass losses occur (Hammerstrom et al. 2006). It is likely that there is high variability among species and within species at different locations in their capacity for sexual reproduction and the creation of seed banks. *Halodule uninervis* meadows off Townsville produce dense seed banks (Inglis 2000), for example, yet meadows of the same species off nearby Cairns have no or limited seed banks (Rasheed 2004). For the majority of seagrass meadows in the region little is known of their capacity for sexual and asexual reproduction, the investment made in maintaining seed banks, or the temporal variation in seed banks and seed production despite this being critical information in determining their resilience and capacity for recovery from impact.

Because of the stochastic nature in the timing and location of tropical storms and the lack of baseline and monitoring data on seagrass it is difficult to assess the damage to seagrass, the recovery cycle and recovery processes, and to provide advice to coastal management agencies on recovery. Our study uses the results of a long term (2008-2012) monitoring and research program at Abbot Point Queensland, that had been initiated in response to a development proposal. This monitoring program fortuitously enabled both a trend analysis of impacts and recovery of seagrasses, and also the experimental tools to understand the processes occurring. We use this information to contrast the recovery of shallow inshore and deep water seagrass meadows. We examine the relative contribution of asexual and sexual reproduction as mechanisms for recovery among the different seagrass species through manipulative experiments and seed bank assessments that were being undertaken when the storm occurred. Together these studies were used to provide a novel insight into the varying ability and mechanisms of different tropical seagrass meadows to recover from large scale storm related losses

Methods

Study area

Abbot Point is on the eastern coast of north Queensland, 25kms north-west of Bowen township (Fig. 1). Seagrass monitoring was conducted between Abbot Point and Euri Creek. Abbot Point is located in Queensland's tropical region and typically experiences a summer wet season (December to March) with an average annual rainfall of 890mm. Air temperatures range from a mean monthly minimum of 13.3°C in July to a mean monthly maximum of 31.5°C in January. The Don River drains the watershed that flows into the study area.

Total annual rainfall and local river flow during the study period were well above the long term averages reflecting the strong La Niña weather system during 2010 & 2011 (Figs. 2, 3).

The offshore and coastal substrate surrounding Abbot Point is open silty/sand. Seagrass communities are the dominant benthic habitat feature, sheltered from oceanic conditions by the Great Barrier Reef (GBR). Eight species of seagrass have been identified in the region with *Halophila* spp. dominating the deeper offshore areas and *Halodule uninervis* dominating the inshore coastal areas (Lee Long et al., 1993; Rasheed et al., 2005). *Halodule uninervis* and *Halophila* spp. are considered to be relatively rapid colonisers and all have fast clonal growth rates (Rasheed 2004). However *Halophila* is a smaller growing species that is shallow rooted with comparatively much smaller stores of energy than *Halodule uninervis.* As a consequence *Halophila* tends to have a lower resilience to impacts and can be highly seasonal and ephemeral. The seagrass meadows in the study were patchy and variable in density. Seasonal variation of above-ground biomass has been reported for the area with a spring/summer maxima and a winter minima (Unsworth et al., 2010).

Seagrass sampling

Seagrass above-ground biomass (g DW m^{-2}) and species composition were assessed at five shallow inshore seagrass meadows and three deeper offshore areas approximately quarterly between May 2008 and September 2012. The shallow meadows were dominated by *Halodule uninervis* and *Zostera mulleri sub sp. capricorni* and the deeper offshore meadows by *Halophila decipiens* and *Halophila spinulosa* which are typical assembleges in shallow and deep water habitats in the GBR region.

Sampling sites at shallow meadows (to approximately 6m below mean sea level (MSL)) were located along transects perpendicular to the shoreline, extending approximately 1km offshore. Assessments were made at approximately 20-100m intervals along each transect or where major changes in bottom topography occurred with additional sites sampled randomly between transects. Transects within meadows were placed approximately 100m apart from each other with the total number of transects dependent on the size of the meadow.

Within each of the three deep water sites (deeper than 6m below MSL) three replicate blocks were assessed with three 100 m transects randomly placed within each block. Deep water sites were surveyed using a sled towed real time closed circuit television (CCTV) camera system. At each sampling site, the camera system was towed for 100 m at drift speed (approximately one knot) and footage observed and recorded. The camera was mounted on a sled that incorporated a sled net 600mm wide and 250mm deep with a 10mm-mesh aperture. Surface benthos was captured in the net and used to confirm seagrass presence and species composition. The technique ensured a large area of seafloor was observed at each site so that patchily distributed seagrass that typifies deep water habitats in the region could be detected. Ten randomly assigned frames were selected from the video record of each 100m transect for seagrass biomass assessment.

Seagrass above-ground biomass at each sampling site (shallow) or video frame (deep water) was determined by visually estimating biomass as described by Mellors (1991) and Rasheed and Unsworth (2011). This technique involves an observer ranking seagrass biomass within a haphazardly placed 0.25m^2 quadrat at each site. Ranks are made in reference to a series of quadrat photographs of similar seagrass habitats for which above-ground biomass has previously been measured. The relative proportion of the above-ground biomass (percentage) of each seagrass species within each survey quadrat was also recorded. Field biomass ranks were converted into above-ground biomass estimates in grams dry weight per square metre (g DW m^{-2}). Each observer ranked a series of calibration quadrats that represented the range of seagrass biomass in the survey. After ranking, seagrass in these quadrats was harvested and the actual biomass determined in the laboratory. A linear regression was calculated between the observed ranks and the measured above-ground biomass for each individual observer. Observer-specific regression equations were applied to field ranks to convert data to above-ground biomass. The data from each individual observer was only used if the linear regression had an $R^2 > 0.95$. This technique has been successfully used to determine small changes in biomass in a range of empirical field and experimental studies (Coles et al., 2009; Rasheed, 1999; Rasheed, 2004; Unsworth et al., 2012).

Recovery experiments

Two seagrass meadows representative of the range of community types at Abbot Point were selected for experimental manipulations to determine the rate of seagrass recovery, role of sexual and asexual reproduction and the species involved in recolonisation of plots following seagrass removal (Fig. 1). Methods for investigating seagrass recovery after loss/removal developed by Rasheed, (1999; 2004) were adapted and applied to the meadows that were the focus of this study. Experiments were conducted between May 2008 and November 2008 which captured the peak growing season for tropical seagrasses in the region which typically occurs between July and December each year. One of the experimental sites was a shallow inshore meadow (approximately 2 m below MSL) dominated by *Halodule uninervis* while the other site was an offshore deep water meadow (approximately 14 m below MSL) dominated by *Halophila* spp. (Fig. 1). A randomised block design of twelve 0.25 m^2 treatment plots was used at each site. The blocks were located haphazardly within each meadow with 3 replicates of 4 different treatments (Table 1). There were two control treatments where seagrass was left undisturbed, one with a border (CB) isolating the plot from surrounding seagrass and one without (CNB) (Table 1). The two experimental treatments had seagrass material including roots and rhizomes removed, with one having a border isolating the plot from any asexual colonisation from the surrounding meadow (CLB) and the second without a border allowing asexual colonisation to occur (CLNB). The isolation borders were made of aluminium and sunk 250mm into the sediment. The border isolated treatments from asexual colonisation by stopping rhizome extension from seagrass surrounding the plots. To investigate how recolonisation is influenced by the availability of sexual propagules (seeds), recovery of seagrass was compared among plots that have all seagrass plants removed but the seed bank left intact. Recolonisation of all the cleared plots was compared to control plots in each block that were left undisturbed. Seagrass recovery and re-growth within each individual 0.25 m^2 plot was measured using leaf shoot density and visual estimates of above-ground biomass (see Rasheed 1999; 2004). These observations were conducted every three months.

Seed bank assessments

Measurements of the seed bank were conducted by taking sediment cores at experimental study sites. On each of the eight sampling occasions, 12 cylindrical cores (0.02m^2) were taken haphazardly around the study sites and sieved in the laboratory. The 710+ μm fraction was inspected for *Halodule uninervis, Zostera muelleri sub sp. capricorni* and other large seeds, and the 250-710 μm fraction was inspected using a dissecting microscope for *Halophila ovalis, Halophila spinulosa* and

Halophila decipiens seeds. The density of seeds (seeds m^{-2}) was determined using the surface area of the core and the mean number of seeds in the sediment at each sampling event.

Data analysis

Summary statistics for seagrass above-ground biomass at shallow and deep water seagrass meadows were calculated and all values are presented as means ± standard error (SE). All observations were randomly distributed and therefore considered independent observations. Data was $\ln_{(x+1)}$ transformed to improve the assumptions of statistical analyses and a one-way ANOVA performed on seagrass biomass data. A least significant difference (LSD) test was used for pairwise comparisons.

Experimental recovery data was examined using repeated-measures ANOVA. Treatment was the between-subjects term; time (shallow: May, July, September, November; deep: July, September, November) and the treatment-time interaction were within-subjects terms. Assumptions of sphericity for the within-subjects factors were accommodated by (Greenhouse–Geisser) adjustments to original *P*-values (von Ende, 1993). Only the Greenhouse–Geisser values are reported here as the statistical significance ($\alpha = 0.05$) of adjusted and original values was equivalent for all variables. Where behaviour of treatments was of particular interest, shoot density was analysed using a one-way ANOVA at each sampling time to determine the difference between treatments. A least significant difference (LSD) test was used for pairwise comparisons of treatment means when ANOVA indicated there were significant differences ($\alpha = 0.05$). Assumptions of normality and homoscedasticity were verified visually by inspecting residuals. Shoot count data was square-root-transformed to meet the assumptions of statistical analyses.

RESULTS

Seagrass species, distribution and abundance

Eight seagrass species were identified in the study area with *Halophila* spp. dominating the deep water areas and *Halodule uninervis* dominating shallow meadows. Prior to the La Niña-related events of 2010/11 and TC Yasi in February 2011 seagrass biomass at Abbot Point fluctuated seasonally with a minimum at the end of the wet season (autumn) and a maximum in spring/early summer (Fig. 4). Following the La Niña-related events of 2010/11, there were significant losses in the density and distribution of Abbot Point seagrasses. There was recovery at the deep water monitoring areas but not at the shallow meadows (Fig. 4).

Biomass in shallow meadows differed significantly among sampling events ($F_{(8, 271)} = 2.31$, $p<0.05$). Biomass (when seagrass was present) ranged from 0.87 g DW m^{-2} in June 2010 to 3.42 g DW m^{-2} in November 2008 (Fig. 4). Seagrass was absent in shallow meadows from March 2011 through to the conclusion of sampling in September 2012. *H. uninervis* was the dominant species present in four of the shallow meadows and *Z. mulleri sub sp. capricorni* was the dominant species in one shallow meadow.

Seagrass biomass in the deep water areas was highly variable and was significantly different among sampling events ($F_{(13, 312)} = 18.61$, $p<0.001$) ranging from 0.13 g DW m^{-2} in May 2011 to 12.36 g DW m^{-2} in November 2010 (Fig. 4). *Halophila* was the dominant deep water seagrass genus during all sampling events with sites containing a mix of *H. ovalis, H. decipiens* and *H. spinulosa*. Biomass in deep water seagrass meadows peaked in November 2010 then declined significantly following the 2010/2011 La Niña-related floods and TC Yasi (Fig. 4). In contrast to the shallow *H. uninervis* meadows, however, seagrass biomass increased during the 18 months following the 2010/2011 floods and TC Yasi (between March 2011 and September 2012) (Fig. 4). Deepwater seagrass meadow biomass also had major declines following previous cyclones that impacted on the Bowen area in March 2009 (TC Hamish) and March 2010 (TC Ului) (Fig. 4).

Recovery Experiments

Shallow and deep water seagrass meadows differed in their capacity for recovery after experimental disturbance and in the mechanisms employed in recolonising. For the shallow *Halodule uninervis* meadow the prevention of asexual colonisation (bordering) had a significant impact on the recovery of seagrass in cleared plots compared with control plots. In contrast, at the deep water *Halophila* spp. meadow, the prevention of asexual colonisation (bordering) had no significant impact on the recovery of seagrass in cleared plots compared with control plots.

At the shallow *H. uninervis* meadow there was a significant interaction between treatment and time in the repeated measures ANOVA (Table 2). Treatments fell into two distinct groups two months after clearing: uncleared control plots (with and without borders) and cleared plots (with and without borders) (Fig.5; Tables 3, 4). Shoot density in treatments that could be colonised asexually (cleared, no border) recovered to the same density as control plots within four months of clearing (Fig.5; Tables 3, 4). Following this initial recovery shoot density in the cleared unbordered treatments did not increase between September and November 2008, but did increase in control plots (Fig.5; Tables 3, 4) . There was no seagrass recovery in the cleared, bordered treatment plots during the study, indicating there was no successful recovery from seeds (Fig. 5; Table 4). The presence of the border had no effect on seagrass growth in control treatments.

At the deep water *Halophila* spp. meadow there was also a significant interaction between treatment and time in the repeated measures ANOVA (Table 2). The prevention of asexual colonisation (bordering) did not have a significant impact on the rate at which cleared plots were able to recover from seeds alone in comparison to the uncleared control plots. Shoot density in cleared treatment plots (bordered and unbordered) recovered to the same density as the control plots (uncleared) within two months (September 2008) of disturbance (Fig. 6; Tables 5 & 6). Following initial recovery, shoot density in cleared plots remained at the same level as control plots until the end of the study (Fig. 6; Table 6).

Seed sampling

In the deep water seagrass meadows *Halophila* spp. seeds were found at two of the eight sampling events; November 2008 and April 2009. Seed density in November 2008 was 53.08 ± 25.57 seeds m^{-2}, and 61.76 ± 46.36 seeds m^{-2} in April 2009. Shallow meadows dominated by *H. uninervis* had a smaller seed bank. *H. uninveris* seeds were found in November 2008 and April and August 2009 at very low densities ranging from 3.54 seeds to 25.16 ± 9.95 seeds. No *H. uninervis* seeds were found at any site after August 2009. No *Z. muelleri sub sp. capricorni* seeds were found on any sampling events.

DISCUSSION

The results of this study demonstrate that initial recovery of tropical seagrasses from large scale severe disturbances is dependent on the seagrass species and the life history traits of those species at the impacted location. Differences in reproductive strategy and particularly the variable presence of seed banks had a major influence on the recovery observed.

All seagrass meadows at Abbot Point were impacted following TC Yasi and several years of La Niña climate patterns. These losses occurred through physical disturbance and reduced light as the result of floods, with declines to near-zero biomass throughout the study area. However, recolonisation and initial recovery only occurred during the study period in the deep water offshore seagrass meadows, while the shallow inshore meadows did not did not re-establish or show recovery in the timeframe of this study. The deep water meadows were mostly comprised of *Halophila* spp., a genus well-adapted to low light conditions (Fourqurean et al., 2003; Udy and Levy, 2002) but quick to decline when stressed (Longstaff and Dennison, 1999). The life history strategy of *Halophila* spp. means they are also well adapted for recovery once conditions become favourable as they are fast growing and rapid colonisers (Hammerstrom et al., 2006; Rasheed 2004; Unsworth et al., 2010). *Halophila* spp. typically produce large numbers of long lived seeds (Hammerstrom and Kenworthy, 2003; Hammerstrom et al., 2006; McMillan, 1991) which can lie dormant in a sediment "seed bank" for several years. Results of seed bank assessments in our study support this, with seed banks found for these meadows at Abbot Point. The manipulative experiments in our study demonstrated the high capacity for deep water *Halophila* spp. meadows to recruit and recolonise through seeds when asexual colonisation was prevented. In experimental trials, recovery was evident for these species after three months. Similar results have been reported for *Halophila* in other tropical Queensland locations (Rasheed 2004). Our experimental study was conducted during the typical growing season for seagrasses in the region (July-December) so were likely to have produced the fastest recovery times if there were strong seasonal differences in recruitment. Had experimental disturbances occurred at times of the year when seagrass growth and reproduction is lower recovery could potentially have been slower.

The results of this study also highlighted the highly variable and seasonal nature of deepwater seagrass abundance. The largest declines in deepwater *Halophila* biomass in our study were associated with major storm events, with big declines after the 2010/11 cyclones culminating in TC Yasi as well as following other less severe cyclones that influenced the area in March 2009 (TC

Hamish) and March 2010 (TC Ului). However even in the absence of these major storm events recent studies would suggest that there was likely to be a strong decline in deepwater *Halophila* meadows during the wet season around December/January as part of natural seasonal cycles (McCormack et al. 2013).

In contrast, shallow inshore meadows mostly comprising *Halodule uninervis* and *Zostera muelleri* sub sp*. capricorni* did not re-establish or show substantial recovery in the 18 months following TC Yasi, and in manipulative field experiments, plots did not recover when asexual recolonisation was excluded. This was due to the near absence of seeds for these species at Abbot Point. There were no *Z. muelleri* sub sp. *capricorni* seeds found and only very low densities of *H. uninervis* seeds at shallow meadows. The production of seed banks for these species appears to be highly site and location specific, with many meadows elsewhere in Queensland capable of forming large seed banks, such as in nearby Townsville (7,000 seeds m^{-2}) (McKenzie et al., 2010) and Gladstone (700-900 seeds m^{-2}) (McCormack et al., 2012), while other locations had limited or no seed banks similar to Abbot Point (McCormack et al., 2012; Rasheed, 2004). For our study it is unclear if the lack of a seed bank was due to a lack of local seed production or the failure of the seed bank to form due to other factors such as high levels of disturbance from wind and wave action in these shallow areas.

Recovery of the shallow coastal meadows via seed or vegetative fragment dispersal from outside the study area was also likely to be limited, with the nearest substantial meadows that could provide *H. uninervis* and *Z. muelleri sub sp. capricorni* propagules being at Upstart Bay, 50 Kilometres to the north. It is highly likely that these meadows were also impacted in a similar negative manner to those of Abbot Point during the region-wide climate and storm impacts, further reducing the likelihood of nearby meadows providing a source of propagules.

This study indicates reproductive strategy and the availability of seed reserves are a major factor in determining the recovery of meadows from wide-scale loss. Other processes, however, also have the potential to influence seagrass recovery. These include changes to light, salinity, nutrients and sediment chemistry that may be associated with flooding and storm impacts (Campbell & McKenzie 2004; Carlson et al. 1994; Lirman & Cropper 2003; Ralph et al. 2007). Light in particular is a major factor in determining seagrass growth, and long term shifts in available light have the ability to significantly impact on the rate of recovery and species composition of the recovering seagrass community (Rasheed 2000). However at our study location, while a lack of light may have played a significant role in the decline of seagrasses it is unlikely it was a major contributor to the lack of recovery observed as measurements over the July 2011 to January 2012 growing season recorded a mean daily PAR of 16.1 mol m^{-2} d^{-1} (McKenna et al., 2013). This value was likely to be well in excess of the minimum light requirements for these species as determined in other Queensland locations (6 mol m^{-2} d^{-1} Chartrand et al., 2012).

The consequences of variable recovery potential of seagrasses in the GBR region are of particular importance. Recent studies have focused on the multiple anthropogenic threats and cumulative impacts to seagrasses in the region (Coles et al., 2010; Grech et al., 2012; 2013) and highlight the increasing vulnerability of these seagrass resources to impacts. Like most seagrass ecosystems, meadows in the GBR provide a range of important ecosystem functions (Carruthers et al., 2002). The GBR is one of the few locations in the world with viable populations of dugong and healthy green turtle populations which are reliant on seagrass meadows for food (Marsh et al., 2005). The GBR was included in a world heritage area in part because of the presence of these iconic species and their health and survival are key management goals (Lucas et al., 1997). Dugong in particular are entirely reliant on seagrasses for food and the widespread losses of seagrass along the Queensland coast in 2010/11 resulted in substantial dugong mortality (GBRMPA 2011). Understanding that not all seagrass systems in the region will have the same capacity for recovery is essential for effective management strategies for seagrasses and their associated ecosystems and species such as dugong and turtle.

Our study demonstrates that seagrass meadows at different depths respond to storm-related losses in different ways. Some meadows have extensive seed banks and rapid recovery can occur even after complete loss of the physical plants. However, the availability of seeds is both species and location specific and the response to disturbance at one location cannot be generalised to another site despite a similar mix of species. Location, species type, a viable seed bank, and the availability of remaining fragments to initiate asexual recovery will all determine the rate of recovery or whether recovery will occur at all.

Providing adequate advice for the management of seagrass is challenging in tropical regions of the GBR and our knowledge of recovery trajectories is limited for tropical species. Most information for seagrass condition comes from intertidal and shallow subtidal studies and from remote sensing because of the logistic ease of collecting information, and consequently inshore measurements dominate data sets. Recovery at a GBR-wide level is likely to be underestimated if the deep water meadows recover faster than shallow meadows. Tropical areas in Queensland are relatively remote and the tropical storms and floods that have devastated the seagrass meadows also incur logistic issues for a consistent field sampling and experimental regime. The tropical seagrass species present are highly variable, mobile in composition and often seasonal. This study was able to address these issues using information from a long term quarterly sampling program, combined with field experiments designed to understand the processes that explain short and long term trends. As the study was being undertaken when the storms and floods occurred it provided a unique opportunity to analyse impacts, recovery and the processes involved.

Conclusion

This study shows that the trajectory of tropical seagrass recovery from large-scale climatic disturbance is not uniform, but is dependent on the seagrass species and the life history traits of those species at the impacted location. Differences in reproductive strategy and particularly the variable presence of seed banks had a major influence on the recovery observed. In our study this manifested as a difference in recovery between deep and shallow meadows largely due to the different species and their reproductive strategies that were present between the two depths. The results highlight the importance of understanding the varying capacity for recovery, not only between species but also variations within species at different locations. Some meadows had extensive seed banks and recovery occurred even after complete loss of the plants. However, the availability of seeds is both species and location specific, and the response from one site cannot be generalised to another. High reliance on clonal growth in many coastal seagrass meadows in tropical Queensland may result in very slow recovery from major disturbances or may not recover at all, particularly if the frequency of such events increases.

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Tables

Table 1. Description of treatments for recovery experiments.

Treatment	Cleared	Not Cleared	Bordered	Not Bordered	Replicates
Cleared, bordered (CLB)		✓	✓		3
Cleared, not bordered (CLNB)		✓		✓	3
Control, bordered (CB)	✓		✓		3
Control, not bordered (CNB)	✓			✓	3

Table 2. Degrees of Freedom (df), mean squares (MS) and levels of significance (P) for ANOVAs used in repeated-measures analysis of experimental seagrass recovery at the deepwater and shallow experimental sites.

	Shallow experimental site			Deep water experimental site		
	df	**MS**	**P**	**df**	**MS**	**P**
Treatment	3	807.286	<0.05	3	85.431	<0.05
Error	8	71.317		8	17.456	
Time	2.103	360.712	<0.001	1.936	838.958	<0.001
Interaction	6.309	143.191	0.001	5.808	42.697	<0.001
Error	16.824	20.66		15.489	3.38	

Greenhouse-Geisser adjusted probability values are reported for time and interaction

*Data square-root transformed

Table 3. Degrees of Freedom (df), mean squares (MS) and levels of significance (*P*) for ANOVAs to test the effects of treatments on shoot density at the shallow *Halodule uninervis* meadow after experimental clearing.

Source of variation	May 2008			July 2008			September 2008			November 2008		
	df	**MS**	***P***	**df**	**MS**	***P***	**df**	**MS**	***P***	**df**	**MS**	***P***
Between Groups	3	492.94	<0.001	3	259.98	<0.05	3	168.281	<0.05	3	187.214	<0.05
Within Groups	8	2.19		8	42.91		8	36.688		8	32.987	
Total	11			11			11			11		

*Data square root transformed

Table 4. Comparisons of mean shoot densities (shoots m^{-2}) after clearing at the shallow *Halodule uninervis* meadow

Treatment	May 2008 (date of clearing)	July 2008	September 2008	November 2008	May 2009
Clear border	0[a]	233.33[a]	0[a]	58.33[a]	0
Clear no-border	0[a]	116.67[a]	300[b]	250[a]	0
Control border	500[b]	850[b]	283.30[b]	591.67[b]	0
Control no-border	491.67[b]	800[b]	141.70[b]	508.33[b]	0

*Data square-root transformed

Treatments that share the same letter group are not significantly different from each other (LSD)

Table 5. Degrees of freedom (df), mean squares (MS) and levels of significance (*P*) for one-way ANOVAs to test the effects of treatments on shoot density at the deep water *Halohila spp.* meadow after experimental clearing.

Source of variation	July 2008			September 2008			November 2008		
	df	**MS**	***P***	**df**	**MS**	***P***	**df**	**MS**	***P***
Between Groups	3	147.457	<0.001	3	17.217	0.269	3	3.423	0.724
Within Groups	8	5.5		8	10.901		8	7.599	
Total	11			11			11		

*Data square-root transformed

Table 6. Comparisons of mean shoot densities (shoots m^{-2}) after clearing at the deep water *Halophila spp.* Meadow.

Treatment	July 2008 (date of clearing)	September 2008	November 2008	May 2009
Clear, border	0^{a}	250^{a}	458.33^{a}	0
Clear, no-border	0^{a}	316.67^{a}	508.33^{a}	0
Control, border	208.33^{b}	475^{a}	500^{a}	0
Control, no-border	91.67^{b}	316.67^{a}	408.33^{a}	0

*Data square-root transformed

Treatments that share the same letter group are not significantly different from each other (LSD).

Figure captions

Fig 1. Location of Abbot Point seagrass meadows and experimental sites.

Fig. 2. Total annual rainfall (mm) in the Abbot Point region (2005-2012) and long-term annual average (Source: Bureau of Meteorology station no. 33257).

Fig. 3. Total annual river flow (megalitres, ML) of the Don River (2005-2012) and long-term annual average (Source: Department of Environment and Heritage Protection Station no. 121003A) *2012 river flow is for January – July only.

Fig 4. Mean above-ground biomass (g DW m^{-2}, all species pooled) (± standard error) at Abbot Point shallow and deep water seagrass meadows, March 2008 – September 2012 and timing of tropical cyclones (TC) that affected the study area.

Fig. 5. Mean *Halodule uninervis* shoot density (shoots m^{-2}) (± standard error) in treatments at the shallow seagrass meadow following experimental clearance.

Fig. 6. Mean *Halophila spp.* shoot density (shoots m^{-2}) (± standard error) in treatments at the deep water seagrass meadow (± standard error) following experimental clearance.

Fig. 1

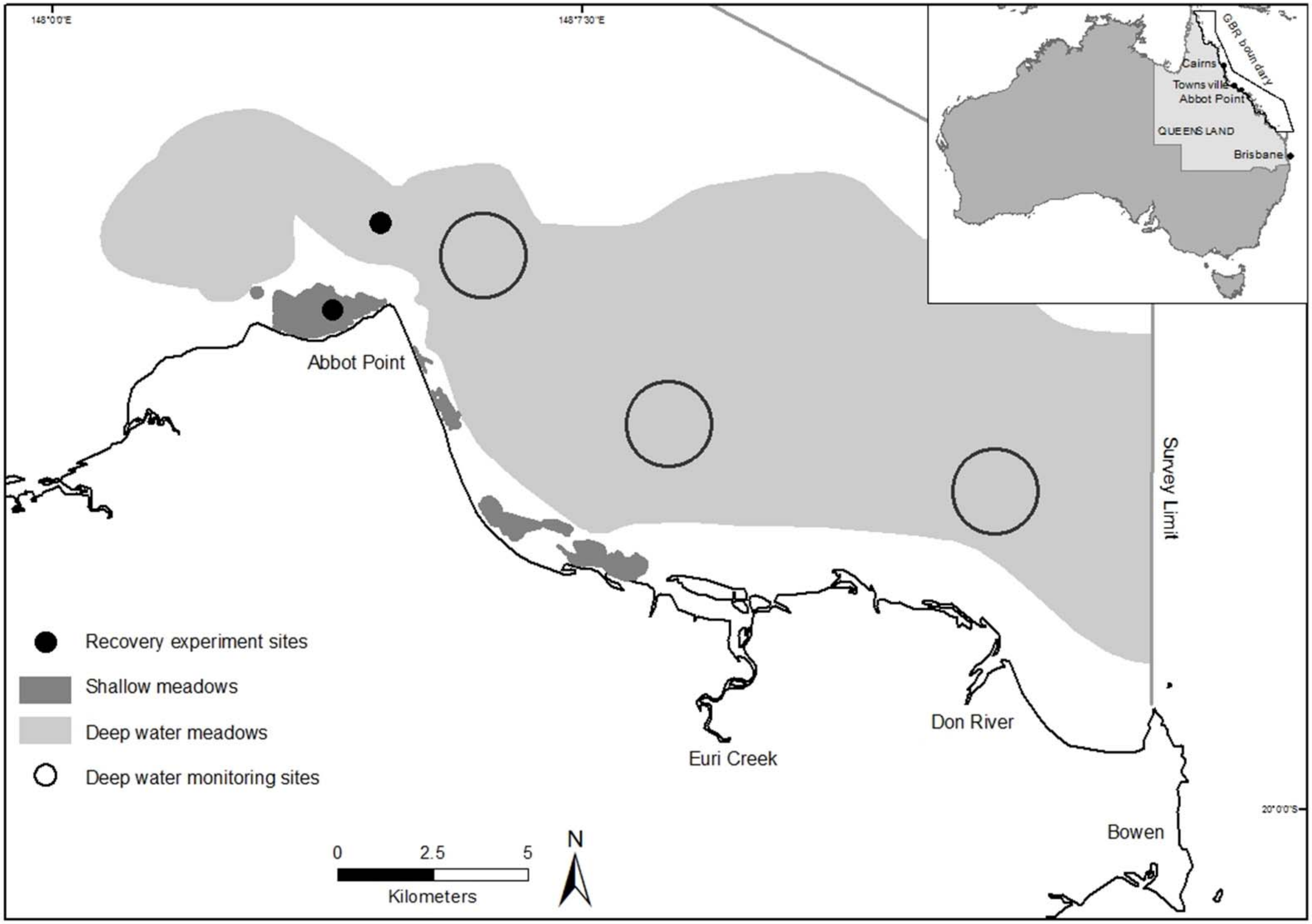
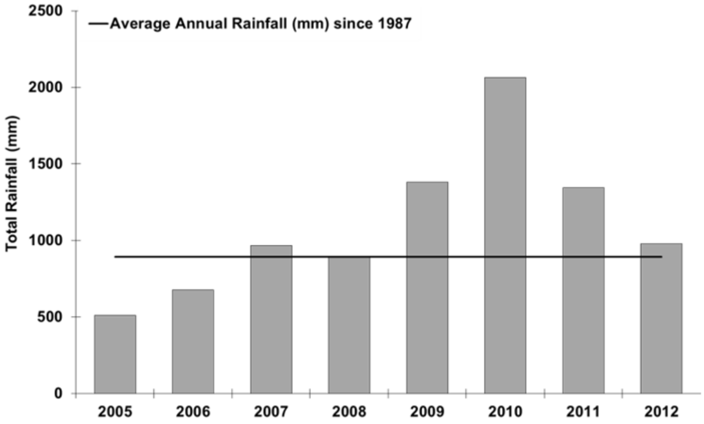
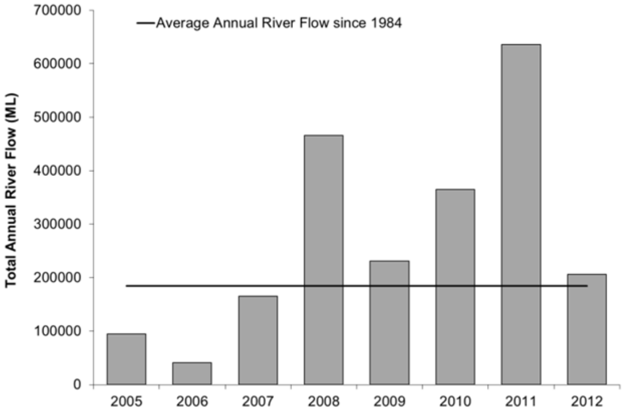

148°0'0"E
148°7'30"E
20°0'0"S
GBR boundary
Cairns
Towns ville
Abbot Point
QUEENSLAND
Brisbane
Abbot Point
Survey Limit
Euri Creek
Don River
Bowen
● Recovery experiment sites
▨ Shallow meadows
▨ Deep water meadows
○ Deep water monitoring sites
0
2.5
5
Kilometers
N

Fig. 2



Average Annual Rainfall (mm) since 1987
Total Rainfall (mm)
2500
2000
1500
1000
500
0
2005
2006
2007
2008
2009
2010
2011
2012

Fig 3.



Average Annual River Flow since 1984
Total Annual River Flow (ML)
700000
600000
500000
400000
300000
200000
100000
0
2005
2006
2007
2008
2009
2010
2011
2012

Fig 4.

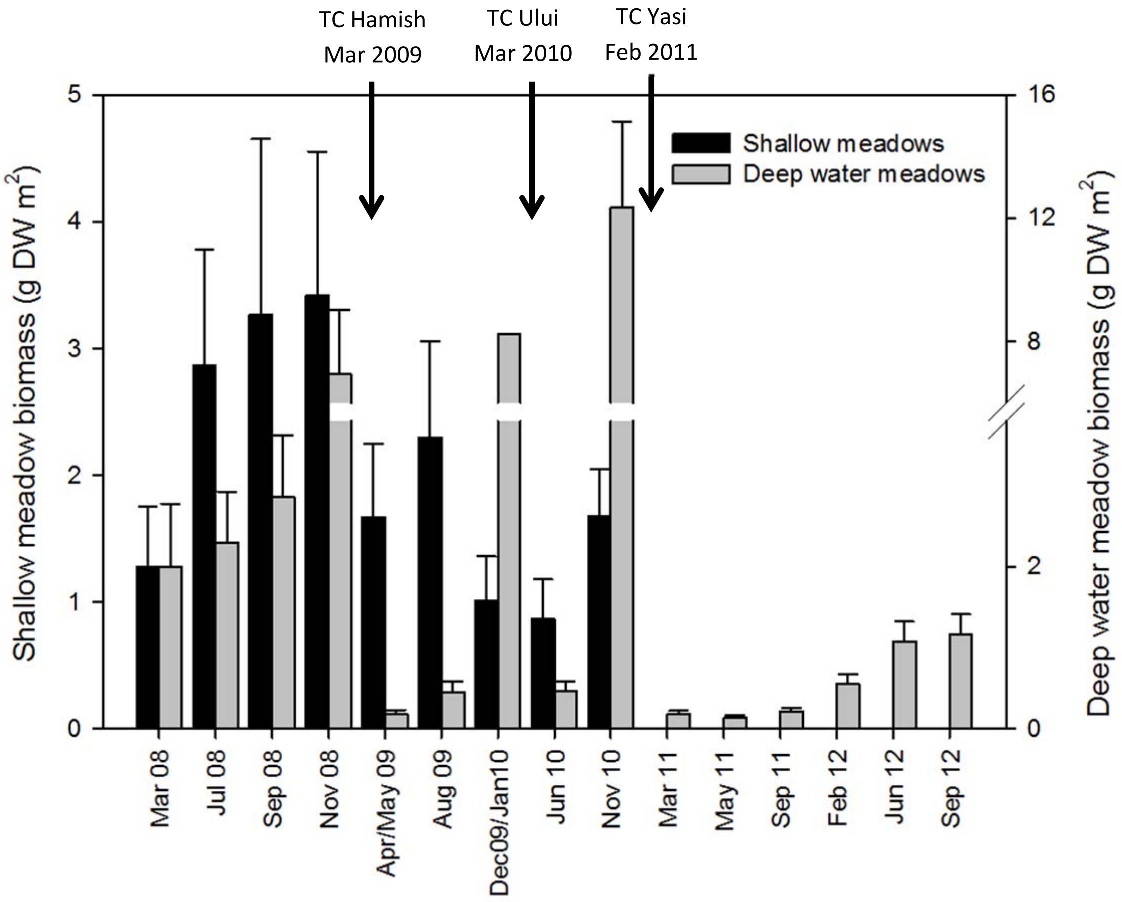

TC Hamish
Mar 2009
TC Ului
Mar 2010
TC Yasi
Feb 2011
Shallow meadows
Deep water meadows
Shallow meadow biomass (g DW m^2)
Deep water meadow biomass (g DW m^2)
0
1
2
3
4
5
0
2
8
12
16
Mar 08
Jul 08
Sep 08
Nov 08
Apr/May 09
Aug 09
Dec09/Jan10
Jun 10
Nov 10
Mar 11
May 11
Sep 11
Feb 12
Jun 12
Sep 12

Fig. 5

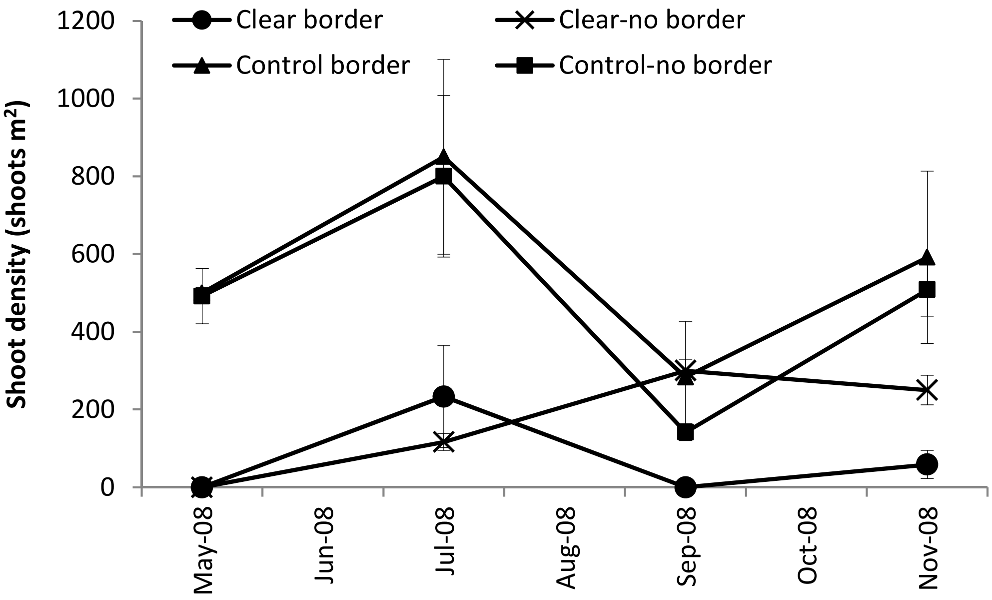
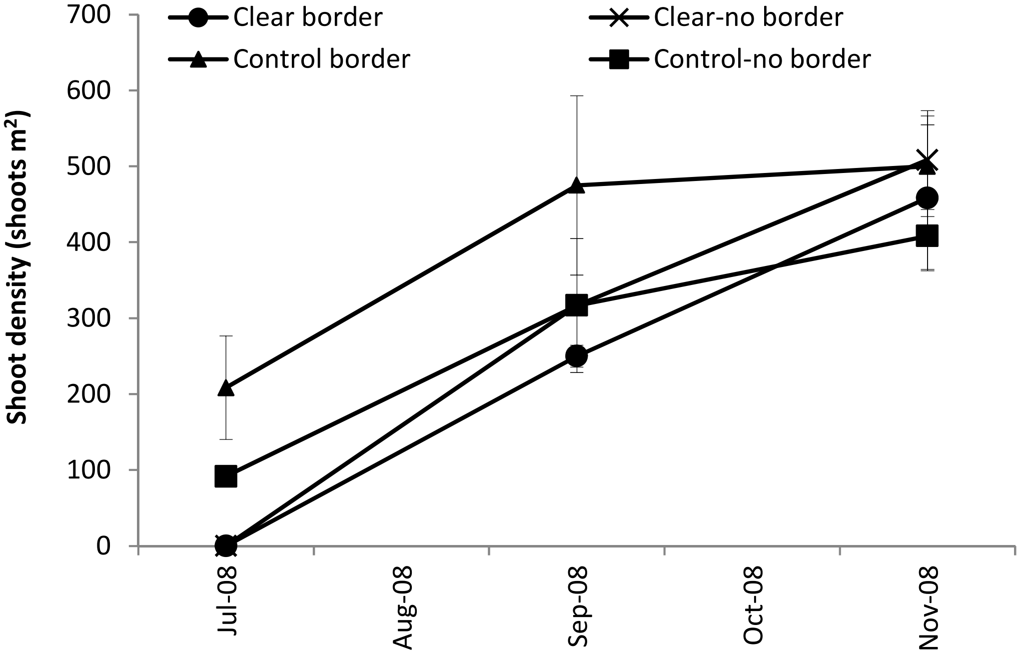

Clear border
Clear-no border
Control border
Control-no border
Shoot density (shoots m^2)
1200
1000
800
600
400
200
0
May-08
Jun-08
Jul-08
Aug-08
Sep-08
Oct-08
Nov-08

Fig. 6



Clear border
Clear-no border
Control border
Control-no border
Shoot density (shoots m²)
700
600
500
400
300
200
100
0
Jul-08
Aug-08
Sep-08
Oct-08
Nov-08