

Phenotypic plasticity promotes persistence following severe events: physiological and morphological responses of seagrass to flooding

Paul S. Maxwell^{1*}, Kylie A. Pitt¹, Dana D. Burfeind^{1,2}, Andrew D. Olds¹,
Russell C. Babcock³ and Rod M. Connolly¹

¹Australian Rivers Institute – Coast and Estuaries and School of Environment Griffith University, Gold Coast, Qld 4222, Australia; ²School of Biological Sciences, University of Queensland, St Lucia, Qld 4072, Australia; and ³Commonwealth Scientific and Industrial Research Organization, Marine and Atmospheric Research, Dutton Park, Qld 4102, Australia

Summary

1. Severe events such as floods or cyclones can have large ecological effects on the structure and functioning of ecosystems. The capacity of an ecosystem to adapt to, or absorb, the effects of a severe event depends on the severity and longevity of the event and the tolerance of the species present.
2. Seagrasses exhibit phenotypic plasticity at the plant to meadow scale through a variety of physiological and morphological acclimations to light stress to enhance photosynthetic capacity. These acclimations provide early warning of the possible risk of larger scale seagrass loss and can therefore be used in predicting how ecosystems might respond to severe events.
3. The physiological and morphological responses of 12 seagrass (*Zostera muelleri*) meadows to a severe flood were examined to test two main hypotheses: (i) that the physiological and morphological characteristics of seagrass would differ between meadows along the established chronic water quality gradient, in a pattern consistent with prior acclimations which have been shown to enhance photosynthetic capacity and (ii) that physiological and morphological responses to the flood would differ between meadows in a manner consistent with their position along the water quality gradient.
4. Meadows had different physiological and morphological characteristics across the water quality gradient, with meadows subject to chronically poorer water quality exhibiting characteristics consistent with those that maximize photosynthetic capacity. Despite a large discrepancy in impact among meadows, all meadows sampled responded consistently to the flood, exhibiting only physiological changes with no significant reduction in biomass. This suggests that photoacclimation to chronically poor conditions can enable seagrasses to withstand the effects of severe events, such as floods.
5. *Synthesis.* Phenotypic plasticity in habitat-forming species can result in a large variation in their responses to severe events, such as floods or cyclones. Acclimation to prior poor environmental conditions can promote persistence in habitat-forming species, such as seagrasses, following severe events. The measurement of phenotypic characteristics along an impact gradient can therefore provide an indication of the response of habitat-forming species to severe events.

Key-words: aquatic plant ecology, habitat-forming species, Moreton Bay, photoacclimation, resilience, water quality gradient, *Zostera muelleri*

Introduction

Severe events such as floods and cyclones have the potential to have large ecological effects from the organism to ecosystem scale, posing significant threats to ecosystem structure, function and ultimately the provision of ecosystem services (Jentsch & Beierkuhnlein 2008). The global human impact on

coastal environments has contributed to calls for greater protection and conservation of marine ecosystems (Gell & Roberts 2003). While initiatives such as pollution minimization and marine reserves are the focus for the majority of conservation strategies, understanding the capacity of ecosystems to absorb and adapt to severe events and retain necessary structures, functions and services has more recently become a key objective of conservation (Suding & Hobbs 2009).

Coastal habitats generally experience multiple types of impacts from chronic disturbances, such as ongoing coastal

*Correspondence author. E-mail: p.maxwell@griffith.edu.au

eutrophication or sedimentation runoff (Thrush *et al.* 2004), but also large-scale, severe episodic floods or cyclones (Coumou & Rahmstorf 2012). Severe events are usually of short duration but can have long-lasting effects on marine ecosystems and thus ultimately affect how they can be best managed (Carpenter *et al.* 2012). They are considered to play a disproportionately large role in determining ecosystem structure and function (Jentsch & Beierkuhnlein 2008), so with forecast increases in the frequency and magnitude of such events (Coumou & Rahmstorf 2012), there is a pressing need to better understand the effects they have on ecosystems (Smith 2011).

The capacity of an ecosystem to adapt to or absorb the effects of a severe event depends on the severity and longevity of the event (Barrett *et al.* 2008) and the tolerance range of the species present (Beierkuhnlein *et al.* 2011). Once the capacity to absorb impact is exhausted, severe events can have sudden and long-lasting effects, often pushing ecosystems over thresholds towards other regimes (Allen & Breshears 1998) where recovery may be prolonged or not possible (Beisner, Haydon & Cuddington 2003). To predict how ecosystems might respond to severe events, it is critical that we understand the processes that promote adaptation. Understanding these processes is particularly important in dominant, habitat-forming species that provide the basis for whole ecosystems (Arnone *et al.* 2011).

In soft sediment coastal areas, seagrasses are common habitat-forming species (Larkum, Orth & Duarte 2006). One of the central paradigms in seagrass ecology is that they provide high-value ecological services (Costanza *et al.* 1997), so with global seagrass loss accelerating (Waycott *et al.* 2009), an understanding of how seagrass ecosystems will respond to the increasing incidence of severe events has become more important (Orth *et al.* 2006). Seagrasses are effective indicators of ecological stress as they integrate environmental impacts over different time-scales (Longstaff *et al.* 1999), are found in both tropical and temperate regions (Short *et al.* 2007) and inhabit those coastal zones closest to anthropogenic and natural impacts (Orth *et al.* 2006). Seagrasses are phenotypically plastic and exhibit high intraspecific variability in morphology (Abal *et al.* 1994; Udy & Dennison 1997) and physiology (Collier *et al.* 2008; Hughes, Stachowicz & Williams 2009) in response to light deprivation, so that their ability to withstand severe events is likely to vary across impact gradients.

This study examined the physiological and morphological responses of *Zostera muelleri* Irmisch ex Aschers., a widespread seagrass species, to the largest flood in 37 years (van den Honert & McAneney 2011), experienced by Moreton Bay, eastern Australia, in January 2011. Previous floods in Moreton Bay in 1974 (Kirkman 1978) and in nearby Hervey Bay in 1992 (Preen, Lee Long & Coles 1995) and 1999 (Campbell & McKenzie 2004) preceded the loss of extensive areas of seagrass in these regions so developing an understanding of the biological stress indicators is useful for detecting negative effects before losses occur. Morphological and physiological parameters are useful early warning indicators for detecting the effect of impacts (Longstaff & Dennison

1999; Collier *et al.* 2008, 2009). This is based on the understanding that seagrasses respond to stress initially with physiological changes prior to morphological changes and, after prolonged light deprivation, eventual mortality (Waycott, Longstaff & Mellors 2005). The potential for seagrass mortality following a severe event is a function of the duration of the event and the ability of the species to survive light deprivation through changes in physiology and morphology (Longstaff & Dennison 1999). When light deprived, changes in photosynthetic efficiency improves light capture (Dennison & Alberte 1985; Abal *et al.* 1994) so the ability to acclimate physiologically to variable light conditions is an advantage for near-shore coastal species such as seagrass. The ability to survive a severe event therefore may also be a function of the physiological and morphological characteristics that have resulted from the long-term chronic water quality conditions present prior to the event.

The physiological responses to light deprivation that have been reported for seagrass are common to many seagrass species and include increased total chlorophyll content to maximize light capture (Dennison & Alberte 1985; Abal *et al.* 1994); decreased ratio of chlorophyll *a* to *b* to improve light absorbance efficiency (Longstaff *et al.* 1999); reduced $\delta^{13}\text{C}$ signature of leaves due to preferential uptake of the lighter ^{12}C (Grice, Loneragan & Dennison 1996), storage of carbohydrate in rhizomes to sustain growth and respiration (Burke, Dennison & Moore 1996); and increased maximum quantum yield (MQY) that indicates an increase in photosynthetic efficiency (Beer *et al.* 2001).

Following physiological changes, morphological responses to light deprivation can maximize the exposure of the photosynthetic apparatus to light while minimising respiratory demands (Lee & Dunton 1997). Morphological responses of seagrass to sublethal light deprivation include increased leaf height (Bulthuis 1983) and leaf width (Lee & Dunton 1997) and decreased leaf (Ruiz & Romero 2003) and shoot density (Abal *et al.* 1994).

In this study, we examined the physiological and morphological responses of 12 *Z. muelleri* meadows to a severe flood to test two main hypotheses: (i) that the physiological and morphological characteristics of seagrass would differ between meadows along the established chronic water quality gradient, in a pattern consistent with prior acclimations which have been shown to enhance photosynthetic efficiency, and (ii) that physiological and morphological responses to the 2011 flood would differ between meadows in a manner consistent with their position along the water quality gradient.

Materials and methods

STUDY AREA AND TIMING

Moreton Bay in south-east Queensland, Australia, is a subtropical shallow coastal embayment that contains a mosaic of coastal habitats (Olds *et al.* 2012a). It is impacted by multiple stressors that operate along multiple gradients (Tibbetts, Hall & Dennison 1998; Bennett, Peterson & Gordon 2009). The Bay is bordered on its eastern side by

three sand islands that allow exchange with oceanic water through three passages (Fig. 1). In the west, the Bay is bordered by the mainland from which four main river estuaries discharge. There is a strong water quality gradient across the Bay with elevated nutrients and poor light availability in the western and southern zones adjacent to riverine discharge (EHMP 2010). In contrast, the eastern zones of the Bay that are proximal to the oceanic passages are typically nutrient limited with saturating light levels and low water residence times. The Brisbane River is the largest river discharging into Moreton Bay (Fig. 1) and typically contains nutrient and sediment levels well above local and national water quality guidelines (EHMP 2010). The majority of flow from the Brisbane River runs north from the mouth into the western embayments. The river impacts seagrass meadows in Deception Bay to the north and Waterloo Bay to the south of the river mouth via a small channel (Dennison & Abal 1999). All sampling was conducted in meadows of eelgrass, *Z. muelleri*, the dominant species in the Bay (Roelfsema *et al.* 2009). Sampling was standardized to a depth of 0.5–1.0 m below lowest astronomical tide and conducted in the middle of individual meadows at least 10 m from meadow edges. As the tidal range in Moreton Bay is approximately 1.5–2.0 m, maximum submergence of seagrasses at the highest astronomical tide is approximately 2.5–3 m. Surveys were conducted four times throughout 2011 (February, May, August, December), in periods of neap tides, following the major Brisbane River flood in January 2011. Twelve meadows were sampled, chosen to encompass the pre-existing

gradient of water quality in Moreton Bay (EHMP 2010; Fig. 1), with the intent of also capturing a range of exposures to flood waters. The most flood-affected meadows in our study were proximal to river estuaries and were therefore also exposed to chronically poor water quality (EHMP 2010). These meadows, however, were not subjected to the main flow from the river mouth and therefore did not suffer any visible effects from scouring.

WATER QUALITY SAMPLING TO DETERMINE LEVEL OF FLOOD IMPACT

Water quality data were collected adjacent to each meadow sampled in the study to assess the level of flood impact. The data were sourced from a local monitoring programme (e.g. see program website EHMP) which collects monthly water quality samples in Moreton Bay. To quantify the level of flood impact, we used a combination of benthic salinity, Secchi disc depth and total nitrogen (TN). These indicators were chosen as representative of freshwater inflow (benthic salinity), water clarity and hence light penetration (Secchi disc depth) and nutrient load (TN). Poor water quality was defined as lower benthic salinity and Secchi disc depth, and higher TN. The January 2011 water samples that are referred to in the results were taken the week following the storm event that led to the flood.

PHYSIOLOGICAL CHARACTERISTICS

In each sampling period, 15 cores (13.5 cm diameter) of *Z. muelleri* were collected haphazardly from each meadow, rinsed clean of sediment and stored frozen. In the laboratory, several indicators of physiological status were measured: non-structural rhizome carbohydrates (sugar and starch), leaf carbon stable isotope ratios, leaf chlorophyll concentration (*a+b*) content, ratio of chlorophyll *a* to *b* and MQY.

Non-structural carbohydrates were extracted from six cores from each meadow. Approximately 15 cm of rhizome material was separated from roots and leaves and dried at 60 °C for 96 h then ground to a powder. Twenty milligrams of the powder from each core was analysed for soluble sugar following the method of Dubois *et al.* (1956). Briefly, sugars were removed from the ground tissue, with two sequential 20-min extractions in 80% ethanol at 60 °C. Sugar content of the extract was determined by the phenol-sulphuric acid colorimetric method using sucrose as a standard. Following extraction of the soluble sugars, the starch content of the remaining material was extracted using perchloric acid according to Quarmby & Allen (1989).

Stable isotope ratios were analysed in two leaves from each of four cores from each meadow. Epiphytes were carefully scraped from the second youngest leaf from two shoots from each core. Samples were dried, ground and analysed with an Isoprime isotope ratio mass spectrometer. The ratio of $^{13}\text{C}/^{12}\text{C}$ was expressed as the relative per mill (‰) difference between the samples and international standard (Pee-Dee belemnite limestone carbonate equivalent).

Maximum quantum yield was measured *in situ* using a diving pulse-amplitude modulated (PAM) fluorometer (Walz, Effeltrich, Germany). Measurements were made on the youngest mature leaf on six shoots per meadow, 1–2 cm from the top of the leaf sheath (lower-mid section). All epiphytic tissue was removed, and the leaf was dark adapted for 5 min (Beer *et al.* 2001) and held 5 mm from the tip of the fibre-optic cable in a dark-adaptation clip to measure the MQY. The 5-min dark-adaptation period was selected following a trial comparison with leaves dark adapted for 10 min. No significant difference was found between the two treatment times (*t*-test; $n = 6$, $t = 2.22$, $P = 0.43$).

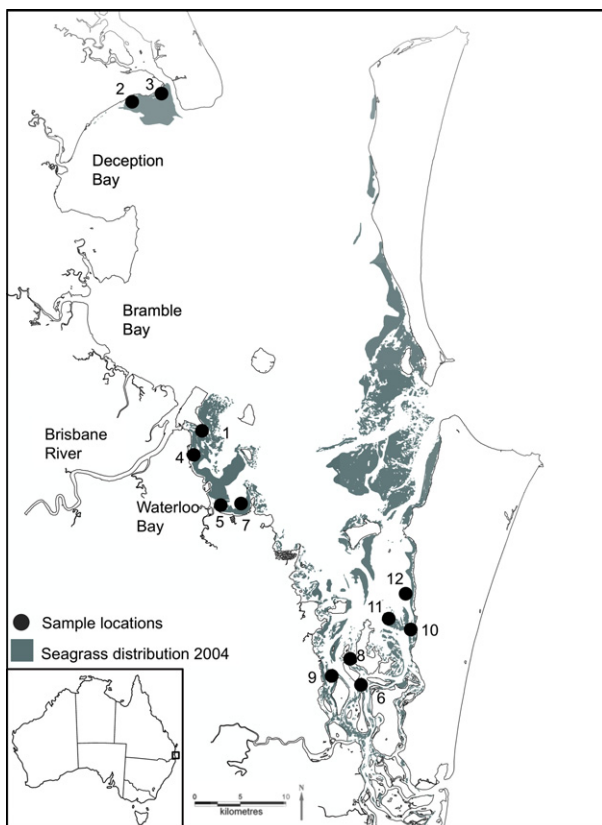


Fig. 1. Map of Moreton Bay showing locations of *Zostera muelleri* meadows sampled following the 2011 Brisbane River flood. The flood plume heavily impacted meadows in Deception and Waterloo Bays. Numbers adjacent to site markers denote their flood impact rank, calculated using water quality data immediately post-flood (January 2011) and combined into one score using principal components analysis (PCA).

Maximum quantum yield was calculated for photosystem II by measuring background fluorescence (F_0) and maximum fluorescence (F_m) after providing a 0.8-s saturating pulse and using the formula $MQY = (F_m - F_0)/F_m$.

Chlorophyll *a* and *b* were extracted from two leaves from each of six cores at each meadow. Epiphytes were carefully scraped from the second youngest leaf from two shoots from each core. A 1-cm² section from each leaf was cut, measured and ground in a mortar and pestle in 10 mL of 90% acetone (after Abal *et al.* 1994). The sample was left for 24 h in the dark at 4 °C and then centrifuged for 20 min at 3600 rpm. The absorbance of the supernatant was measured by a spectrophotometer at 750, 663 and 645 nm and the concentrations of chlorophyll *a* and *b* calculated (Dennison 1990).

MORPHOLOGICAL CHARACTERISTICS

Above-ground tissue was separated from below-ground tissue in six cores from each meadow. The number of leaves and shoots was counted, and the average leaf height and width per core was recorded. Epiphytes were carefully scraped from each leaf. Samples were then dried at 60 °C for 48 h and weighed to get above- and below-ground biomass. Epiphyte biomass was intended to be included in the analysis; however, the amount removed was very small for all meadows so the analysis was terminated after the first two sample periods.

STATISTICAL ANALYSIS

Three types of analyses were carried out on water quality data: (i) to illustrate the magnitude of the 2011 flood relative to background water quality conditions, the three water quality parameters (benthic salinity, Secchi depth, TN) averaged over 3 months (January, February and March) were compared for each year (fixed) from 2002 to 2011, and meadow (fixed), with permutational multivariate analysis of variance (PERMANOVA; Anderson, Gorley & Clarke 2008). The results were illustrated using canonical analysis of principal components (CAP). This method maximizes the separation between significant factors of interest (Anderson & Willis 2003). (ii) To determine the exposure of the 12 meadows to flood waters, each meadow was ranked according to the water quality conditions in the week following the rainfall that caused the flood in January 2011. The rank was based on the principal components analysis (PCA) score calculated from the three water quality parameters in January 2011. (iii) To determine how water quality differed between meadows over time following the flood, the three water quality parameters were compared between meadows and sampling periods with a two-way PERMANOVA with month (fixed) and meadow (fixed) as factors.

Physiological and morphological characteristics were analysed separately, but using the same methods. Each group of characteristics was analysed together to examine temporal variation using PERMANOVA. Month was the factor (fixed), and water quality (collected in January 2011 post-flood) was a covariate to test for correlation with each group of seagrass characteristics and to examine how they interacted with temporal variation. To do this, a principal component analysis (PCA) score was calculated for each meadow and sampling month, based on Euclidean ($\log x + 1$) similarity measures. If the Month factor in the PERMANOVA was significant, Tukey's *post hoc* tests were performed to identify differences between months. BEST analyses (Clarke, Somerfield & Gorley 2008) were used to identify the parameters primarily responsible for causing differences over time. All multivariate analyses were based on Euclidean ($\log x + 1$) similarity measures, which include joint absences and are therefore appropriate

for examining environmental impacts (Anderson *et al.* 2011). Additionally, for each parameter, the mean of all months for each meadow was correlated (Pearson) with January 2011 water quality (right hand panels in Figs 6 and 7) and one-way ANOVA conducted to assess differences between months (left hand panels in Figs 6 and 7).

Results

COMPARISON OF POST-FLOOD WATER QUALITY TO LONGER-TERM WATER QUALITY CONDITIONS

The January 2011 flood had a significant negative effect on water quality in Moreton Bay. Multivariate analysis demonstrated that water quality in the 3 months following the flood in 2011 was significantly poorer than water quality in the same 3 months for every other year since 2002 ($F = 16.84$, $P = 0.001$; Fig. 2, see Table S1 and S2 in Appendix S1 in Supporting Information). Long-term water quality was significantly different between meadows ($F = 11.34$, $P = 0.001$, Table S1) with water quality poorer at meadows closest to the Brisbane River than at meadows further away (Fig. 3 and Table S2).

VARIATION IN WATER QUALITY CONDITIONS POST-FLOOD

Water quality varied between the 12 meadows following the flood ($F = 6.12$, $P = 0.047$; Fig. 4, Table S3). Water quality was poorest at meadows in northern Waterloo Bay, immediately adjacent to the Brisbane River mouth, and in northern Deception Bay (for site rankings based on January 2011 water quality see Fig. 1). Meadows further from the river mouth in the south eastern bay had the best water quality (Table S4).

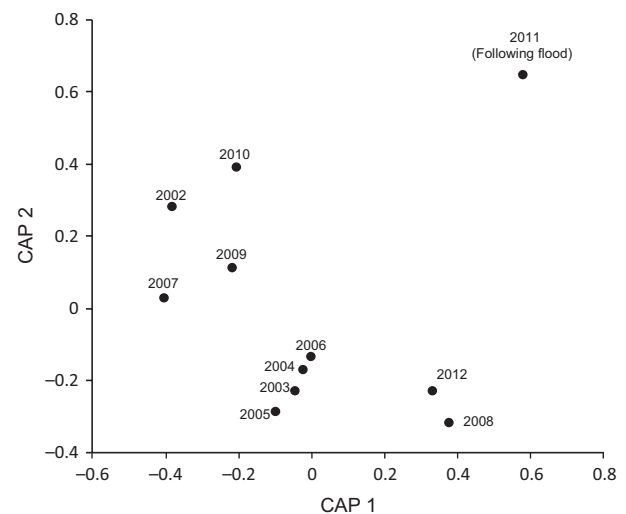


Fig. 2. Summer water quality variation between years since 2002 in Moreton Bay. Data were collected from sites adjacent to each of the 12 seagrass meadows. Points are centroid values for each year based on three water quality parameters: salinity, Secchi depth (indicating water clarity) and total nitrogen collected once a month from January, February and March each year. The centroid value is calculated using canonical analysis of principal coordinates (CAP; Table S2).

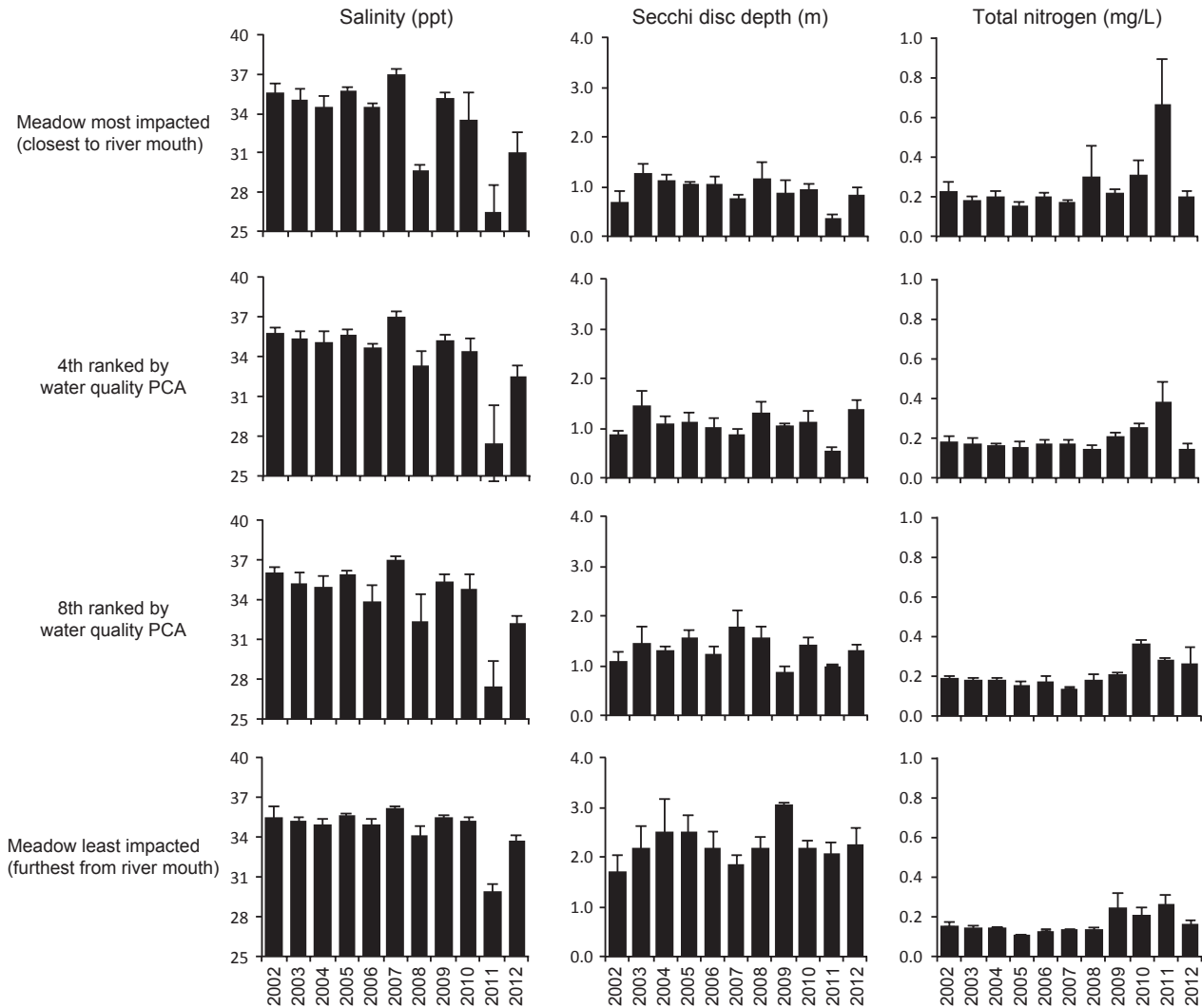


Fig. 3. Water quality data collected from sites adjacent to each meadow. Data shown are the mean of the data collected in January, February and March for each year since 2002 for four of the 12 meadows (showing the most flood-impacted meadow, the four and eight most impacted and least flood-impacted meadow on rankings based on January 2011 data; Table S2).

Water quality differed significantly between sampling months ($F = 32.51$, $P = 0.004$; Table S3), with water quality the poorest following the flood, improving throughout winter (May and August sampling) and declining again with summer rainfall in December (Table S4 and Fig. 5).

PHYSIOLOGICAL CHARACTERISTICS

Seagrass physiological characteristics differed significantly between months ($F = 4.29$, $P = 0.001$; Fig. 6a, Table S5) and co-varied significantly across the water quality gradient ($F = 11.74$, $P = 0.001$; Fig. 6b, Table S5). There was no interaction between month and water quality ($F = 0.72$, $P = 0.199$). All months differed significantly from each other (Table S6). Sugar levels, starch levels, carbon isotope signature ($\delta^{13}\text{C}$), total chlorophyll and the ratio of chlorophyll a:b explained the majority of the variation between months (BEST, $P = 0.01$, $\rho = 0.877$). MQY did not make significant contributions to the model and will not be discussed further.

Rhizome sugar levels were lowest immediately following the flood and increased throughout the year (Fig. 6c). Sugar levels were highest at meadows with the lowest flood impact ($R^2 = 0.51$, $P = 0.033$; Fig. 6d). Starch levels at all sites were highest in February, were significantly lower in August and returned to initial levels by December (Fig. 6e). Starch levels were generally highest in meadows with the poorest chronic water quality and most impacted by the flood ($R^2 = 0.46$, $P = 0.015$; Fig. 6f). Rhizome starch concentrations were the dominant non-structural carbohydrate. The leaf carbon isotope ratio ($\delta^{13}\text{C}$) increased following the flood with February samples significantly lower than all other sampling periods (Fig. 6g). $\delta^{13}\text{C}$ were lowest at meadows with the poorest chronic water quality and most impacted by the flood ($R^2 = 0.75$, $P = 0.008$; Fig. 6h). Total leaf chlorophyll concentrations were highest in February, declined throughout winter and increased in December to levels recorded in February (Fig. 6i). Total chlorophyll values were highest at meadows with the poorest chronic water quality and most

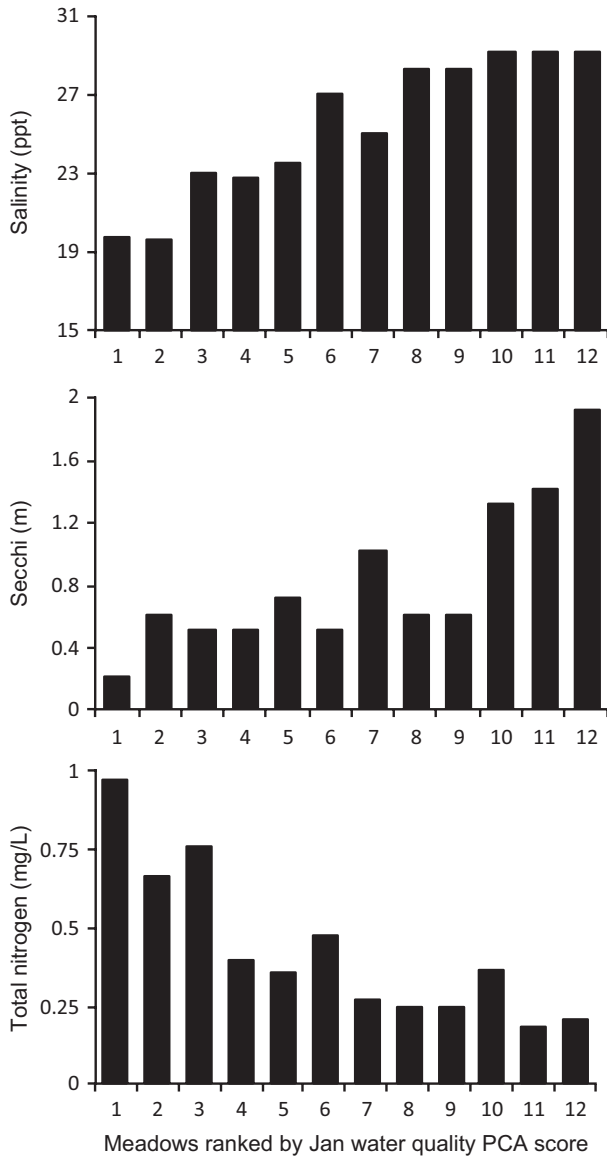


Fig. 4. Flood water quality adjacent to each meadow. Data are from January 2011 immediately following the flood, for the three water quality parameters: salinity, Secchi depth (indicating water clarity) and total nitrogen, combined into one score using principal components analysis (PCA) and used to rank each of the meadows from most impacted (1) to least impacted (12) (Table S4).

impacted by the flood ($R^2 = 0.41$, $P = 0.024$; Fig. 6j). The ratio of leaf chlorophyll *a:b* was lowest in February and December and peaked in May and August (Fig. 6k). Chlorophyll *a:b* ratios were lowest at meadows with the poorest chronic water quality and most impacted by the flood ($R^2 = 0.48$, $P = 0.031$; Fig. 6l).

MORPHOLOGICAL CHARACTERISTICS

The morphological characteristics of *Z. muelleri* meadows following the January 2011 flood differed significantly amongst meadows across the water quality gradient ($F = 3.12$, $P = 0.031$; Fig. 7a and Table S7), but did not differ between

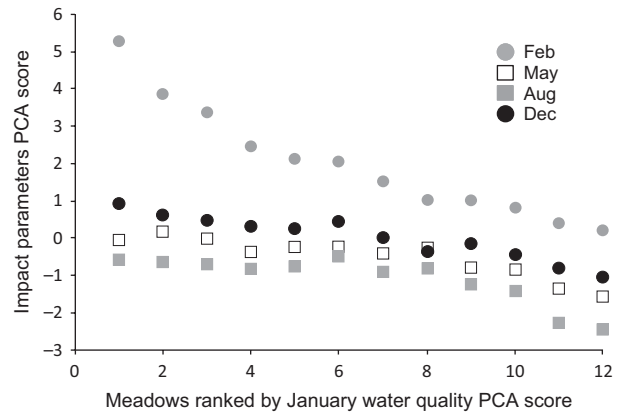


Fig. 5. Water quality variation from the four sampling months throughout 2011 following the flood in January. The data from three water quality parameters; salinity, Secchi disc depth (indicating water clarity) and total nitrogen is illustrated using principal components analysis (PCA) and used to rank each of the meadows from most impacted (1) to least impacted (12) (Table S4).

sampling periods following the flood ($F = 1.36$, $P = 0.209$; Fig. 7b). There was no interaction between meadow and sampling period factors ($F = 0.69$, $P = 0.705$). Three of the variables (above-ground biomass (AGBM; Fig. 7c,d), below-ground biomass (BGBM; Fig. 7e,f) and leaf height (Fig. 7g,h) best explained the variation across flood impact levels (BEST, $P = 0.01$, $\rho = 0.94$). For each of these variables, values generally increased with increasing flood impact level (AGBM, $R^2 = 0.47$, $P = 0.036$; BGBM, $R^2 = 0.54$, $P = 0.048$; leaf height, $R^2 = 0.55$, $P = 0.006$). The remaining morphological parameters did not make significant contributions to the model (Fig. 7i–l) and will not be discussed further.

Discussion

To predict the responses of ecosystems to severe events, it is necessary to understand the processes that promote acclimation, particularly for dominant engineering species that provide a basis for whole ecosystems (Arnone *et al.* 2011). Our results indicate that phenotypic plasticity within habitat-forming species such as *Z. muelleri* can play an important role in determining how they withstand severe events. We demonstrate that *Z. muelleri* acclimates to chronically poor water quality by changing physiological and morphological characteristics and respond to severe events, such as floods, through physiological responses. In the year following the flood in 2011, there was no mortality of *Z. muelleri* in meadows we sampled. The overall pattern of responses was of physiological acclimations consistent with light deprivation. Physiological characteristics varied between meadows along the water quality gradient and changed consistently at all meadows throughout the year, despite the large discrepancy in impact intensity along the water quality gradient. We did not detect changes in morphology following the flood; however, the most impacted meadows exhibited physiological and morphological characteristics consistent with seagrasses having

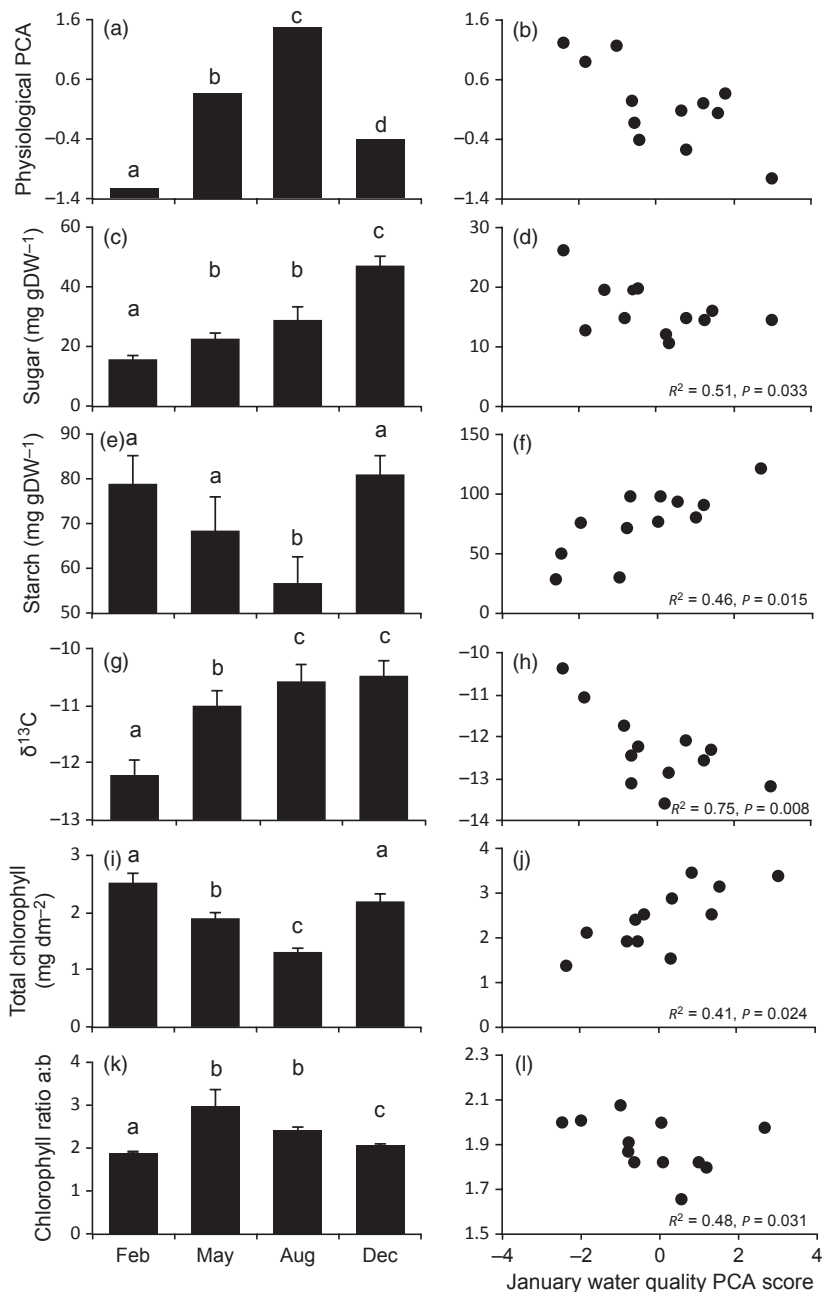


Fig. 6. Variation in key physiological characteristics of meadows following the January 2011 flood including; (a–b) principal components analysis (PCA) score for physiological variables for each month and meadow to illustrate the results of the PERMANOVA (Table S5 and S6); (c–d) rhizome sugars; (e–f) rhizome starch; (g–h) carbon isotope ratio; (i–j) total chlorophyll concentration; and (k–l) chlorophyll ratio a:b. Left side panels show the mean (\pm SE) of all meadows per sampling month, different letters indicate significantly different means in post hoc tests. Right side panels show mean of all meadows for all months sampled, plotted against level of flood impact (defined as water quality sampled from each meadow immediately following the January 2011 flood). R^2 and P values given where the relationship is significant. NS denotes not significant.

optimized their photosynthetic capacity (Longstaff *et al.* 1999; Collier *et al.* 2008, 2009).

Phenotypic plasticity like that we describe here enables species to cope with varying degrees of stress to avoid mortality (Miner *et al.* 2005) and has become a key factor in understanding the distribution and diversity of organisms along impact gradients (Valladares, Gianoli & Gómez 2007). Generally, short-term physiological plasticity can allow an organism to acclimate to highly temporally variable environmental conditions, with longer-term morphological responses contributing to variation in suitable habitat-forming species (Sultan *et al.* 1998). Species that lack sufficient plasticity to maintain growth and reproduction in degraded and variable environments might be at risk of range reductions or localized extinctions (Sultan 2000). Plasticity can affect a range of direct

(e.g. responses to temperature or increased herbivory) and indirect (e.g. trait-mediated effects on predation or grazing rates which cascade to other species) interactions between organisms and their environment and ultimately affect ecological processes and functioning (Miner *et al.* 2005). Phenotypic plasticity can be ecologically advantageous for habitat-forming species, with the persistence of such species following severe events likely to promote ecosystem stability (Lloret *et al.* 2012).

The physiological and morphological plasticity of *Z. muelleri* meadows may help them withstand severe weather events; however, it is probable that the relatively short duration of poor conditions, which followed the 2011 flood, also contributed to the persistence of *Z. muelleri* meadows in Moreton Bay. The length of time seagrasses can withstand periods of

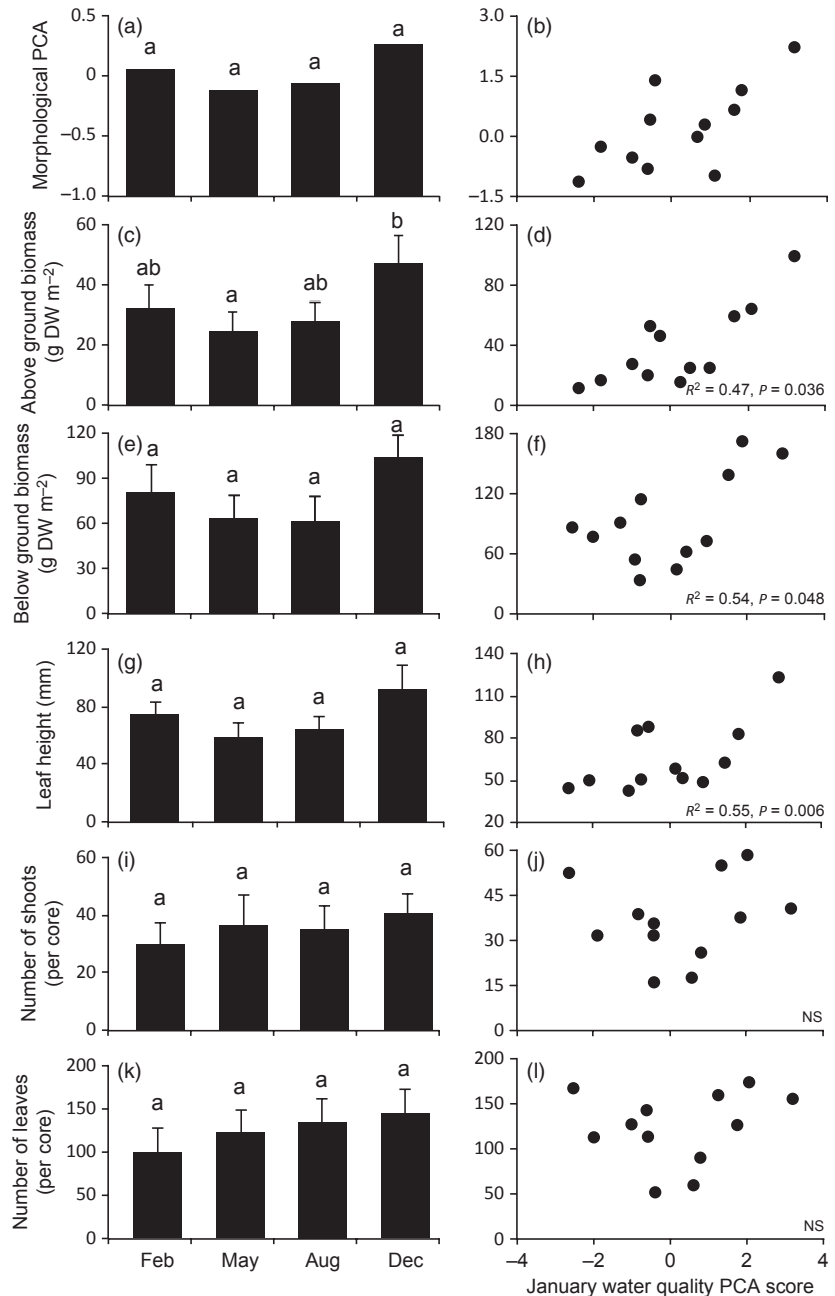


Fig. 7. Variation in the morphological characteristics of meadows following the January 2011 flood (Table S7); (a) principal components analysis (PCA) score for morphological variables for each month and (b) site, plotted against the January water quality PCA score (an indicator of level of flood impact). Panels (a) and (b) illustrate the results of the PERMANOVA. Higher January PCA scores denote poorer water quality. Morphological characteristics varied significantly across the water quality gradient (Table S7) but did not vary over the four sampling months. Above-ground biomass (c,d), below-ground biomass (e,f) and leaf height (g,h) best explained the variation across the water quality gradient. Shoot (i-j) and leaf (k-l) density did not differ between months or across the water quality gradient. R^2 and P values given where the relationship is significant. NS denotes not significant.

light deprivation depends on the species studied. For fast growing and opportunistic species such as *Halophila ovalis*, biomass can decline after 3–6 days, with total shoot loss within as little as 21 days (Longstaff *et al.* 1999). Larger, longer-lived species (e.g. *Posidonia sinuosa*) can persist for 3–6 months (Gordon *et al.* 1994). For *Z. muelleri*, Abal *et al.* (1994) showed that plants survived after 2 months of near total light deprivation. Water quality in Moreton Bay returned to background levels within 2 months of the flood at the most impacted meadows and within a month at the least impacted meadows (see EHMP website), which falls within the temporal limits of light deprivation tolerance for *Z. muelleri* (Abal *et al.* 1994). Had the weather conditions following the flood resulted in a more extended period of poor water clarity, or resulted in

a second flood, it is possible that there would have been significant declines in seagrass biomass or large-scale meadow loss similar to that experienced previously in Hervey Bay, a similar coastal embayment in the region. In 1992, Hervey Bay experienced two flood plumes in 3 weeks resulting in 90% seagrass loss (Preen, Lee Long & Coles 1995). In 1999, Hervey Bay experienced a single flood with a 2- to 3-fold increase in turbidity and nutrients that persisted for 6 months, resulting in 95% loss of seagrass meadows (Campbell & McKenzie 2004). The duration and frequency of floods also alter community structure in other ecosystems, negatively affecting plant biomass and species composition in wetlands (Casanova & Brock 2000), and freshwater stream communities (McCabe & Gotelli 2000). In both examples, higher-frequency

and longer-duration floods selected for species are able to tolerate variable and poor conditions.

The physiological mechanisms that prolonged the persistence of *Z. muelleri* in our study are similar to those described for other seagrass species: *Posidonia oceanica* (Alcoverro, Manzanera & Romero 2001), *P. sinuosa* (Collier *et al.* 2008, 2009), *Thalassia testudinum* (Lee & Dunton 1997) *Halophila ovalis* (Longstaff *et al.* 1999) and *Halodule pinifolia* (Longstaff & Dennison 1999). The decreasing levels of stored starch following light deprivation reported here concur with experiments on other *Zostera* species (Alcoverro *et al.* 1999; Brun *et al.* 2008) and other tropical species in Queensland (e.g. *Halodule pinifolia* and *Halophila ovalis*; Longstaff *et al.* 1999), showing that starch levels decrease in response to light deprivation. The utilization of carbohydrate stores can sustain seagrasses, while they are exposed to prolonged light deprivation (Dennison & Alberte 1986; Burke, Dennison & Moore 1996). Based on these studies, we expected that the most flood-impacted meadows would have lower carbohydrate reserves than those less impacted, due to chronically low light levels. Our results showed the opposite, however, with the meadows most exposed to the flood and poor water quality having more than double the levels of starch recorded in less impacted meadows (Fig. 6f). This confirms that *Z. muelleri* can photoacclimate to the lower light conditions typically found in the western Bay regions (EHMP 2010). We infer that this characteristic of impacted meadows in the Bay played a significant role in their persistence following the flood.

The starch to sugar ratio in *Z. muelleri* recorded in this study is much higher than that found in temperate *Zostera* species such as *Z. marina* (e.g. Burke, Dennison & Moore 1996; Vichkovitten, Holmer & Frederiksen 2007) and *Z. noltii* (Vermaat & Verhagen 1996), where soluble sugars are the dominant stored carbohydrate. This could simply reflect differences between species but could also reflect differences between subtropical and temperate regions, since in the latter, seasonal gains and losses in photosynthetically derived carbohydrate supply stem from highly seasonal light fluctuations. In contrast, previous studies in Moreton Bay have shown little seasonal variation in seagrass biomass (Boon, Moriarty & Saffigna 1986), which most likely results from a less-pronounced seasonal trend in light availability (Longstaff 2003).

The leaf carbon isotope ratio ($\delta^{13}\text{C}$) increased at all meadows as conditions improved. This is similar to previous experimental studies of local seagrass species that showed that the $\delta^{13}\text{C}$ signature of seagrass leaves decreased during light deprivation (Abal *et al.* 1994; Grice, Loneragan & Dennison 1996; Longstaff *et al.* 1999). This is probably due to the preferential uptake of ^{12}C over ^{13}C in low light as less energy is expended in the process (Longstaff *et al.* 1999) and a greater total demand for carbon at higher light intensities that lessens discrimination among the isotopes and leads to a greater relative uptake of ^{13}C (Grice, Loneragan & Dennison 1996). An alternative explanation for the reduced $\delta^{13}\text{C}$ in the meadows most impacted by poor water quality is input to the meadow of ^{13}C deplete carbon from decomposing terrestrial

organic matter (Hemminga & Mateo 1996). Seagrass meadows adjacent to mangrove forests, for example, can have lower $\delta^{13}\text{C}$ signatures than meadows further away (Bouillon, Connolly & Lee 2008). The more negative $\delta^{13}\text{C}$ signatures we recorded immediately following the flood and the subsequent increase through the year may also reflect the decreasing influence of the flood run-off over time.

The 2011 flood in Moreton Bay was one of the larger floods in the past 100 years (van den Honert & McAneney 2011). However, when compared to the severe deleterious effects that the previous large flood in 1974 had on seagrasses (Kirkman 1978) and corals (Lovell 1989) in Moreton Bay, both habitats have persisted with minimal ill effects from the 2011 event (Olds *et al.* 2012b). It is possible that this is because the 1974 flood plume persisted for longer than in 2011; however, it is also possible that the existing distribution of seagrass in Moreton Bay has been reduced to areas not as heavily impacted by the poorest conditions following severe flood events. The majority of seagrass loss in the Bay has occurred in Bramble and Deception Bays, the regions most impacted by river run-off (Dennison & Abal 1999). Despite this, with the predicted increase in episodic rainfall and severe events for south-east Queensland (CSIRO 2007; Cai & Rensch 2012), the existing seagrass meadows of Moreton Bay remains at high risk.

Severe events, such as floods, have the capacity to exert disproportionately large effects on the structure and functioning of ecosystems (Jentsch & Beierkuhnlein 2008). Nevertheless, our results indicate that physiological and morphological diversity within habitat-forming species, such as *Z. muelleri*, can play an important role in determining their capacity to withstand such events. Phenotypic plasticity of the type we recorded can increase the length of time seagrass can persist below minimum light requirements (Abal *et al.* 1994; Grice, Loneragan & Dennison 1996). This may explain why seagrass biomass, shoot or leaf density did not decline following the flood, particularly in the meadows most impacted by the flood plume. The broad physiological and morphological variation between seagrass meadows in the study area suggests wide tolerance in the responses of *Z. muelleri* to periods of light deprivation. This plasticity is likely to be a key aspect of its long-term survival and dominance along the tropical east coast of Australia. It is also anticipated to be critical for the persistence of other habitat-forming species after severe disturbance events.

Acknowledgements

This work was funded by a Water Science scholarship (PSM) from the Australian Rivers Institute, and an Australian Research Council grant (RMC and KAP) in collaboration with CSIRO (RCB) and the Queensland Department of Science, Information Technology, Innovation and Arts. We thank A. Grinham and two anonymous referees for helpful comments regarding the article.

References

- Abal, E., Loneragan, N., Bowen, P., Perry, C., Udy, J. & Dennison, W. (1994) Physiological and morphological responses of the seagrass *Zostera capricorni*

- Aschers, to light intensity. *Journal of Experimental Marine Biology and Ecology*, **178**, 113–129.
- Alcoverro, T., Manzanera, M. & Romero, J. (2001) Annual metabolic carbon balance of the seagrass *Posidonia oceanica*: the importance of carbohydrate reserves. *Marine Ecology Progress Series*, **211**, 105–116.
- Alcoverro, T., Zimmerman, R.C., Kohrs, D.G. & Alberte, R.S. (1999) Resource allocation and sucrose mobilization in light-limited eelgrass *Zostera marina*. *Marine Ecology Progress Series*, **187**, 121–131.
- Allen, C.D. & Breshears, D.D. (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 14839–14842.
- Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, UK.
- Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511–525.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L. *et al.* (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.
- Arnone, J.A. III, Jasoni, R.L., Lucchesi, A.J., Larsen, J.D., Leger, E.A., Sherry, R.A., Luo, Y., Schimel, D.S. & Verburg, P.S.J. (2011) A climatically extreme year has large impacts on C4 species in tallgrass prairie ecosystems but only minor effects on species richness and other plant functional groups. *Journal of Ecology*, **99**, 678–688.
- Barrett, J.E., Virginia, R.A., Wall, D.H., Doran, P.T., Fountain, A.G., Welch, K.A. & Lyons, W.B. (2008) Persistent effects of a discrete warming event on a polar desert ecosystem. *Global Change Biology*, **14**, 2249–2261.
- Beer, S., Björk, M., Gademann, R. & Ralph, P.J. (2001) Measurements of photosynthetic rates in seagrasses. *Global Seagrass Research Methods* (eds F.T. Short & R. Coles), pp. 183–198. Elsevier, Amsterdam.
- Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E. & Kreyling, J. (2011) Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology*, **99**, 703–713.
- Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003) Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, **1**, 376–382.
- Bennett, E.M., Peterson, G.D. & Gordon, L.J. (2009) Understanding relationships among multiple ecosystem services. *Ecology Letters*, **12**, 1394–1404.
- Boon, P.L., Moriarty, D. & Saffigna, P.G. (1986) Nitrate metabolism in sediments from seagrass (*Zostera capricorni*) beds of Moreton Bay, Australia. *Marine Biology*, **91**, 269–275.
- Bouillon, S., Connolly, R.M. & Lee, S.Y. (2008) Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. *Journal of Sea Research*, **59**, 44–58.
- Brun, F.G., Olivé, I., Malta, E.J., Vergara, J.J., Hernández, I. & Pérez-Lloréns, J.J. (2008) Increased vulnerability of *Zostera noltii* to stress caused by low light and elevated ammonium levels under phosphate deficiency. *Marine Ecology Progress Series*, **365**, 67–75.
- Bulthuis, D.A. (1983) Effects of in situ light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *Journal of Experimental Marine Biology and Ecology*, **67**, 91–103.
- Burke, M., Dennison, W. & Moore, K. (1996) Non-structural carbohydrate reserves of eelgrass *Zostera marina*. *Marine Ecology Progress Series*, **137**, 195–201.
- Cai, W. & Rensch, P. (2012) The 2011 southeast Queensland extreme summer rainfall: a confirmation of a negative Pacific Decadal Oscillation phase? *Geophysical Research Letters*, **39**, L08702.
- Campbell, S.J. & McKenzie, L.J. (2004) Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. *Estuarine, Coastal and Shelf Science*, **60**, 477–490.
- Carpenter, S., Arrow, K., Barrett, S., Biggs, R., Brock, W., Crépin, A.-S. *et al.* (2012) General resilience to cope with extreme events. *Sustainability*, **4**, 3248–3259.
- Casanova, M.T. & Brock, M.A. (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology*, **147**, 237–250.
- Clarke, K.R., Somerfield, P.J. & Gorley, R.N. (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, **366**, 56–69.
- Collier, C.J., Lavery, P.S., Ralph, P.J. & Masini, R.J. (2008) Physiological characteristics of the seagrass *Posidonia sinuosa* along a depth-related gradient of light availability. *Marine Ecology Progress Series*, **353**, 65–79.
- Collier, C.J., Lavery, P.S., Ralph, P.J. & Masini, R.J. (2009) Shade-induced response and recovery of the seagrass *Posidonia sinuosa*. *Journal of Experimental Marine Biology and Ecology*, **370**, 89–103.
- Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V. & Paruelo, J. (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.
- Coumou, D. & Rahmstorf, S. (2012) A decade of weather extremes. *Nature Climate Change*, **2**, 491–496.
- CSIRO (2007) *Climate Change in Australia – Technical Report 2007*. CSIRO, Canberra.
- Dennison, W.C. (1990) Chlorophyll content. *Seagrass research methods* (eds R.C. Phillips & C.P. McRoy), pp. 83–86 UNESCO, USA.
- Dennison, W.C. & Abal, E.G. (1999) *Moreton Bay Study: A Scientific Basis for the Healthy Waterways Campaign*. South East Qld Regional Water Quality Management Strategy Team, Brisbane.
- Dennison, W.C. & Alberte, R.S. (1985) Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). *Marine Ecology Progress Series*, **25**, 51–61.
- Dennison, W.C. & Alberte, R.S. (1986) Photoadaptation and growth of *Zostera marina* L. (eelgrass) transplants along a depth gradient. *Journal of Experimental Marine Biology and Ecology*, **98**, 265–282.
- Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P. & Smith, A.M. (1956) Colorimetric method for determination of sugars and related substances. *Analytical Chemistry*, **28**, 350–356.
- EHMP (2010) *Ecosystem Health Monitoring Program 2008–09 Annual Technical Report*. South East Queensland Healthy Waterways Partnership, Brisbane.
- EHMP (2013) *Ecosystem Healthy Monitoring Program*. <http://www.healthywaterways.org/ehmp/home.aspx> [accessed 22 March 2013].
- Gell, F.R. & Roberts, C.M. (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, **18**, 448–455.
- Gordon, D.M., Grey, K.A., Chase, S.C. & Simpson, C.J. (1994) Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading. *Aquatic Botany*, **47**, 265–275.
- Grice, A., Loneragan, N. & Dennison, W. (1996) Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. *Journal of Experimental Marine Biology and Ecology*, **195**, 91–110.
- Hemminga, M.A. & Mateo, M.A. (1996) Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. *Marine Ecology Progress Series*, **140**, 285–298.
- van den Honert, R.C. & McAneney, J. (2011) The 2011 Brisbane floods: causes, impacts and implications. *Water*, **3**, 1149–1173.
- Hughes, A.R., Stachowicz, J.J. & Williams, S.L. (2009) Morphological and physiological variation among seagrass (*Zostera marina*) genotypes. *Oecologia*, **159**, 725–733.
- Jentsch, A. & Beierkuhnlein, C. (2008) Research frontiers in climate change: effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience*, **340**, 621–628.
- Kirkman, H. (1978) Decline of seagrass in northern areas of Moreton Bay, Queensland. *Aquatic Botany*, **5**, 63–76.
- Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (2006) *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht.
- Lee, K.S. & Dunton, K.H. (1997) Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex Kijning. *Journal of Experimental Marine Biology and Ecology*, **210**, 53–73.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, **18**, 797–805.
- Longstaff, B.J. (2003) *Investigations into the Light Requirements of Seagrasses in Northeast Australia*. PhD thesis, University of Queensland, Brisbane.
- Longstaff, B.J. & Dennison, W.C. (1999) Seagrass survival during pulsed turbidity events: the effects of light deprivation on the seagrasses *Halodule pinnifolia* and *Halophila ovalis*. *Aquatic Botany*, **65**, 105–121.
- Longstaff, B., Loneragan, N., O'Donohue, M. & Dennison, W. (1999) Effects of light deprivation on the survival and recovery of the seagrass *Halophila ovalis* (R. Br.) Hook. *Journal of Experimental Marine Biology and Ecology*, **234**, 1–27.
- Lovell, E.R. (1989) Coral assemblages of Moreton Bay, Queensland, Australia, before and after a major flood. *Memoirs of the Queensland Museum*, **27**, 535–550.
- McCabe, D.J. & Gotelli, N.J. (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia*, **124**, 270–279.
- Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. & Relyea, R.A. (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution*, **20**, 685–692.

- Olds, A., Connolly, R.M., Pitt, K.A. & Maxwell, P.S. (2012a) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series*, **462**, 191–203.
- Olds, A., Pitt, K.A., Maxwell, P.S. & Connolly, R.M. (2012b) Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology*, **49**, 1195–1203.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L. Jr, Hughes, A.R., Kendrick, G.A., Kenworthy, W.J. & Olyarnik, S. (2006) A global crisis for seagrass ecosystems. *BioScience*, **56**, 987–996.
- Preen, A.R., Lee Long, W.J. & Coles, R.G. (1995) Flood and cyclone related loss, and partial recovery, of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany*, **52**, 3–17.
- Quarmby, C. & Allen, S.E. (1989) Organic constituents. *Chemical Analysis of Ecological Materials* (ed. S.E. Allen), pp. 172–176. Blackwell Scientific, Oxford.
- Roelfsema, C., Phinn, S., Udy, N. & Maxwell, P. (2009) An integrated field and remote sensing approach for mapping seagrass cover, Moreton Bay, Australia. *Journal of Spatial Science*, **54**, 45–62.
- Ruiz, J.M. & Romero, J. (2003) Effects of disturbances caused by coastal constructions on spatial structure, growth dynamics and photosynthesis of the seagrass *Posidonia oceanica*. *Marine Pollution Bulletin*, **46**, 1523–1533.
- Short, F., Carruthers, T., Dennison, W. & Waycott, M. (2007) Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology*, **350**, 3–20.
- Smith, M.D. (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology*, **99**, 656–663.
- Suding, K.N. & Hobbs, R.J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution*, **24**, 271–279.
- Sultan, S.E. (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, **5**, 537–542.
- Sultan, S.E., Wilczek, A.M., Bell, D.L. & Hand, G. (1998) Physiological response to complex environments in annual *Polygonum* species of contrasting ecological breadth. *Oecologia*, **115**, 564–578.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Ellis, J.I., Hatton, C., Lohrer, A., Norkko, A. (2004) Muddy water: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment*, **2**, 299–306.
- Tibbetts, I.R., Hall, N.J. & Dennison, W.C. (1998) *Moreton Bay and Catchment*. School of Marine Science, University of Queensland, Brisbane.
- Udy, J.W. & Dennison, W.C. (1997) Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. *Journal of Experimental Marine Biology and Ecology*, **217**, 253–277.
- Valladares, F., Gianoli, E. & Gómez, J.M. (2007) Ecological limits to plant phenotypic plasticity. *New Phytologist*, **176**, 749–763.
- Vermaat, J.E. & Verhagen, F.C.A. (1996) Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. *Aquatic Botany*, **52**, 259–281.
- Vichkovitten, T., Holmer, M. & Frederiksen, M.S. (2007) Spatial and temporal changes in non-structural carbohydrate reserves in eelgrass (*Zostera marina* L.) in Danish coastal waters. *Botanica Marina*, **50**, 75–87.
- Waycott, M., Longstaff, B.J. & Mellors, J. (2005) Seagrass population dynamics and water quality in the Great Barrier Reef region: a review and future research directions. *Marine Pollution Bulletin*, **51**, 343–350.
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L. & Hughes, A.R. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 12377–12381.

Received 31 July 2013; accepted 23 September 2013

Handling Editor: John Lee

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Results of all PERMANOVA tests and pairwise comparisons.

Table S1. Spatial and temporal variation in long-term water quality conditions (results of PERMANOVA).

Table S2. Spatial and temporal variation in long-term water quality conditions (results of pairwise tests).

Table S3. Spatial and temporal variation in water quality conditions post-flood (results of PERMANOVA).

Table S4. Spatial and temporal variation in water quality conditions post-flood (results of pairwise tests).

Table S5. Temporal variation in physiological characteristics with water quality covariate (results of PERMANOVA).

Table S6. Temporal variation in physiological characteristics with water quality covariate (results of pairwise tests).

Table S7. Temporal variation in morphological characteristics with water quality covariate (results of PERMANOVA).