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Recovery from the impact of light reduction on the seagrass *Amphibolis griffithii*, insights for dredging management.

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ABSTRACT

A large-scale, manipulative experiment was conducted to examine the extent and rate of recovery of meadows of the temperate Australian seagrass, *Amphibolis griffithii* to different light-reduction scenarios typical of dredging operations, and to identify potential indicators of recovery from light reduction stress. Shade cloth was used to mimic different intensities, durations and start times of light reduction, and then was removed to assess the recovery. The meadow could recover from 3 months of light stress (5-18% ambient) following 10 months re-exposure to ambient light, even when up to 72% of leaf biomass was lost, much faster recovery rates than has previously been observed for large seagrasses. However, when the meadow had been shaded for 6-9 months and more than 82% of leaf biomass was lost, no recovery was detected up to 23 months after the light stress had ceased, consistent with other studies. Five potential indicators of recovery were recommended.

KEYWORDS

dredging, light reduction, recovery, seagrass, *Amphibolis griffithii*, Australia

INTRODUCTION

Dredging can impact coastal marine habitats through direct (e.g. physical removal, spoil dumping) and indirect means (e.g. toxicant release, sedimentation, light reduction), with direct impacts generally easier to predict. Over the past decade, management of dredging has improved significantly, largely through improved ability to predict the spatial extent and intensity of turbid plumes (Je et al., 2007; Lepland et al., 2009; Wu et al., 2007) but also through a greater understanding on the potential impacts on marine biota (Cooper et al., 2008; Cruz-Motta and Collins, 2004; Koslow et al., 2001; Simonini et al., 2005; Skilleter et al., 2006; Ware et al., 2009). However, for some globally important benthic habitats, such as seagrass meadows, the susceptibility to environmental changes caused by dredging is not well understood (Erftemeijer and Robin Lewis III, 2006). Further, while the ability to predict habitat loss is improving, the capacity to predict the loss of ecological function associated with less severe (i.e. sub-lethal) dredging impacts remains poor for many ecosystems, but is of significant concern for full assessment of environmental impacts and in developing mitigation programmes.

Seagrass meadows are a dominant component of most coastal ecosystems and provide important ecosystem services such as primary production, nutrient cycling, sediment stabilization, food and habitat for other organisms and trophic transfers to adjacent habitats (Hemminga and Duarte, 2000). Globally, these ecosystem services have been valued at approximated US$19 000 ha^{-1} yr^{-1} (Costanza et al., 1997). Despite these recognized values, the area of seagrass is reducing world-wide at an alarming and increasing rate (Waycott et al., 2009). Dredging is one of the mechanisms responsible for seagrass loss, directly through physical removal or smothering or indirectly through the creation of turbid plumes which reduce light reaching the benthos (Cabaco et al., 2008; Erftemeijer and Robin Lewis III, 2006; Orth et al., 2006; Waycott et al., 2009). Dredging-related seagrass losses have occurred at scales of km^2 (Orth et al., 2006) and it has been estimated that up to 21 000 ha of seagrass meadow has been lost world-wide in the past 50 years, most

likely an underestimate (Erftemeijer and Robin Lewis III, 2006). In at least half of these cases seagrass loss was associated with dredging (Erftemeijer and Robin Lewis III, 2006).

It is clear that globally dredging impacts highly valued seagrass meadows, leading to losses of seagrass habitat, that is, lethal or acute impacts. However, of equal importance to many impact assessments are the sub-lethal effects of dredging, and these are poorly understood. The sub-lethal effects of dredging include the loss of ecosystem function associated with reduced primary productivity or altered habitat structure, which affect the provision of food and habitat for other organisms. A key concern in assessing the impact of dredging on seagrass ecosystems is the length of time these ecosystem functions are compromised, that is, how long does it take for the ecosystem to recover. Recovery from dredging related stressors, defined as a return to pre-disturbance or undisturbed conditions (Elliott et al., 2007) has been demonstrated (Biber et al., 2009; Collier et al., 2009; Gonzalez-Correa et al., 2005; Hammerstrom et al., 2007), and the rate of recovery depends on a variety of factors (see Pickett and White, 1985) such as the size and severity of the impact (Fonseca et al., 2004) and the seagrass species. Recovery can take years and, in some instances, has been predicted to take centuries (Walker et al., 2006).

Biological indicators are regularly used in other habitats exposed to dredging (Bayer et al., 2008) but they have only recently been developed for a few seagrass species (Collier et al., 2007; Collier et al., 2009; Lavery et al., 2009). To assess biological responses to stress, monitoring of seagrass meadows often involves measures of cover, biomass or shoot density, which indicate change to the habitat once losses have occurred. Early warning indicators of stress would be useful to detect impact and recovery in the habitat before mortality occurs, that is, sub-lethal indicators. These early warning indicators are based on the premise that plants respond to stress along a predicted cause-effect pathway where physiological adjustments (e.g. photosynthetic rate, growth rate) precede morphological adjustments (e.g. leaf loss) and, finally, mortality (Waycott et al., 2005).

Recent research (Lavery et al., 2009) simulated light reduction scenarios (5-19% of ambient light) typical of dredging operations on *Amphibolis griffithii* seagrass meadow. The response to light-

reduction was dependent on the interactive effects of the duration, intensity and time that light reductions were imposed. Short durations (3 months) significantly impacted seagrass meadows (up to 72% loss of leaf biomass) but the severity of the impact depended on the time of year, and the intensity of light reduction. With longer durations of light reduction (6-9 months) the severity of the impact increased (82-100% loss of leaf biomass), and the response at different times of year was more consistent. These insights improved the capacity to manage dredging-related impacts in terms of improved predictive capacity and identification of potential early warning indicators of stress. However, it did not improve our understanding of the capacity of the ecosystem to recover from impact and, therefore, the period of time in which ecosystem services are compromised.

This study will build on the work of Lavery et al. (2009), which assessed the impacts of light reduction. This paper provides new information on the magnitude and speed of recovery of an *Amphibolis griffithii* seagrass meadow from a variety of dredging-related light reduction impacts. It uses the treatments created from the previous experiment (Lavery et al., 2009) to assess the timescales of recovery, where recovery is defined as a return to control conditions. The second aim is to characterize the process of recovery of *Amphibolis griffithii* seagrass, which will aid in identifying potential early indicators of seagrass recovery that could be applied in recovery monitoring programmes.

METHODS

Experimental design

The effect of three factors, the intensity, duration and timing of reduced light (photosynthetic photon flux density:PPFD) was experimentally tested in an extensive (> 6 ha) meadow of the seagrass *Amphibolis griffithii*, in 4.5 m water at Jurien Bay, Western Australian (30° 18′ 34′′ S, 115° 00′ 26′′ E; WGS84 datum) between March 2005 and July 2006 (Lavery et al., 2009). In the present study, the plots established by Lavery et al. (2009) were re-sampled, and a new data-set collected to assess seagrass recovery from the combination of these light reduction treatments.

The levels of each factor are described in Lavery et al (2009) but in brief are as follows: intensity – Control (i.e. ambient PPFD), Moderate (13-19% of ambient) and High (5-11% of ambient); duration (3, 6, 9 months); and timing (Autumn, commencing in March; or Spring, commencing in September). The levels of intensity and the duration were selected to cover the upper range of light reduction encountered during large, commercial dredging operations in the region (e.g. Geraldton Port Authority, unpubl. data). The timing was selected to assess if the impact and recovery from the light reduction was consistent at different times of the year.

In the initial experiment performed to test the effect of light reduction (Lavery et al., 2009), five replicate plots of each treatment (4.5 m x 3 m with an effective sampling area of 3 m x 1.5 m (Mackey et al., 2007)) were established in a fully orthogonal design (n = 120: 2 start times x 4 durations x 3 intensities x 5 replicates), as described in Lavery et al. (2009). At the end of each duration, (3, 6 or 9 mo.) the plots allocated to that duration treatment were sampled and the shade cloth used to reduce the light was removed. This sampling time was subsequently referred to as Recovery duration 0. To generate data for the current study the plots were then re-sampled at a later date to assess the recovery of the seagrass meadow using two approaches. First, for the 3-month duration plots, samples were collected 3 and 10 months after the shade cloths were removed. Consequently, for these plots the recovery period for the Autumn treatments was over winter, summer and autumn (June 2005 – April 2006) and for the Spring treatments summer, autumn, winter and spring (December 2005 – November 2006, Figure 1). The 6- and 9-month duration plots were heavily impacted at the end of shading (Lavery et al., 2009) and no leaves were observed in these plots three months after the shade cloth was removed. Consequently, the period of time before re-sampling these plots was extended, to August 2007, such that the Autumn 6-month plots had 23 months of recovery, Autumn 9-month plots - 21 months, Spring 6-month plots - 17 months and Spring 9-month plots - 15 months of recovery (Figure 1).

Study species

Amphibolis griffithii seagrass is endemic to temperate western and southern Australian coastlines (Ducker et al., 1977), and has a similar morphology to the more widespread seagrass genus *Thalassodendron*. It forms continuous monospecific meadows as well as mixed species, patchy

meadows (Holmes et al., 2007) in sandy and rocky substrates (Carruthers et al., 2007; Ducker et al., 1977). Aspects of *A. griffithii*'s morphology and growth characteristics are important to understand in the context of predicting recovery from impact. *Amphibolis* is placed towards the centre of the seagrass functional form model (Walker et al., 1999). This clonal plant is composed of underground roots and rhizomes with a vertical, branching stem that holds terminal leaf clusters (Cambridge, 1999). There are generally 2-5 leaves per cluster and 6-20 clusters per vertical stem (Cambridge, 1999; Ducker et al., 1977). Stems are long lived, generally 2-3 years (den Hartog, 1970) whilst leaves are much shorter lived, generally 90 days (Marba and Walker, 1999). The plastochrone interval of vertical stems (short shoots or branches of a stem) is 277 days, horizontal rhizome 509 days and leaves 32 days (Marba and Walker, 1999). Upright stems are produced every 4-6 horizontal rhizome internodes and branches are produced every 3-17 vertical stem internodes (Coupland, 1997).

The complex canopy structure of *A. griffithii* meadows provides an ideal environment for algal and faunal epiphytes to colonise (Ducker et al., 1977). Consequently, there is a higher biomass and diversity of algae and fauna living on *A. griffithii* compared to other seagrass species (Borowitzka et al., 1990; Edgar, 1990; Gartner et al., 2010), including a unique assemblage of fish characterised by different species and larger fish than those found in other large seagrass, such as *Posidonia* (Hyndes et al., 2003). Greater predation rates have also been observed in *A. griffithii* meadows compared to *Posidonia* meadows (Vanderklift et al., 2007).

Light and water temperature

Light (PPFD) reaching the top of the seagrass canopy in one plot from each treatment was measured using 'Odyssey Dataflow' submersible incident light sensors, with an automated wiper unit cleaning the sensor every 15 minutes (Carruthers et al., 2001). Instantaneous PPFD (μmol m^{-2} s^{-1}) integrated over a 1 min period was measured every 10 - 15 minutes, throughout the entire experiment. All light loggers were calibrated against a standard light source. During the recovery period light at the top of the canopy was only measured in control plots and a complete set was not obtained for all of the Spring recovery periods. Light data was summarised as average total daily irradiance (mol m^{-2} d^{-1}) and the hours above saturating irradiance (H_{sat}) where, the

saturating light intensity for photosynthesis was set at 55 μmol m^{-2} s^{-1} (Masini and Manning, 1997). Water temperature data were sourced from Department of Environment and Conservation Western Australia (unpublished data), from a regular monitoring site in 5 m depth at 30° 27′ S and 115° 03′ E (WSG84).

Variables measured

For the plots that had been shaded for 3 months, samples were collected and variables measured as described in Lavery et al (2009), and for plots that had been shaded for 6 and 9 months, a sub-set of variables were measured (biomass (g DW m^{-2}) of leaf, stem and algal epiphytes, and canopy height (80^{th} percentile)). Above-ground samples for biomass, density and morphology variables were pooled from five randomly selected 10 x10 cm units taken from within a 50 x 50 cm quadrat (i.e. sample area of 0.05 m^2) located randomly within the effective sampling area of each plot. The number of clusters and leaves in each sample were counted to estimate cluster and leaf density (m^{-2}). A cluster was defined as a group of leaves separated from the next cluster by visible stem. A leaf was counted if it had emerged from the sheath. One stem was randomly selected from each sample to take additional measures of leaf length and width (oldest leaf in cluster) and internode length (five most recently produced internodes). Stem height of all stems was also measured. The number of leaves per cluster was counted for the entire sample, then separated into leaves and stems and all algal epiphytes removed. Each component was dried separately at 60°C for 24 h before weighing. Canopy heights were calculated from the stem height data in the sample.

Leaf growth for the 1-2 week period prior to biomass sampling was estimated by tagging all leaf clusters (~ 30) on 6 stems using the leaf punch method of (Short and Duarte, 2001). Depending on the stems randomly selected, this yielded 10-30 tagged leaf clusters per plot. Leaf extension was calculated as the sum of all leaves that grew in a cluster. Leaf growth measures were only measured during the recovery period after 3 months, not after 10 months.

Six stems with associated below-ground rhizome material were collected separately from within each plot. Leaves were sampled from the mid-canopy, 20-40 cm above the sediment surface. Samples of living leaf and rhizome were scraped free of epiphytes, dried and ground in a mill

grinder. Samples were analysed for carbon (% DW), nitrogen (% DW) $\delta^{13}C$ and $\delta^{15}N$ using a mass spectrometer (ANCA-NT Europa Scientific, Crewe, UK) interfaced with a 20–20 isotope ratio mass spectrometer (Europa Scientific, Crewe, UK). Isotope signatures were determined by comparison with laboratory reference material previously calibrated against IAEA or NIST standard reference materials with a precision of <0.1‰. Soluble sugars (% DW) and starch (% DW) were analysed by colorimetric determination (420 nm) with an amylase pre-digest to convert the starch to glucose (Yemm and Willis, 1954).

Statistical analyses

Although the original impact experiment had a fully orthogonal design (Lavery et al., 2009), analysis of the recovery data was not, as the sampling involved repeated measures of the same plots. A repeated measures ANOVA was used to test for any effect of the recovery period on seagrass variables in the different shading treatments (different intensities, recovery periods and start-times of shading). All analyses were performed using Statistica® v7. Repeated measures ANOVA was used as the treatment plots were re-sampled and were not considered independent. Each duration was analysed separately as the time of the recovery period varied between the 3, 6 and 9 month treatments. Within each duration, each start time was analysed separately. Data were tested for normality using the Kolmogorov-Smironov goodness of fit test (Zar, 1999) and heterogeneity using Cochran's Test (Cochran, 1951) and transformed if necessary. Fishers LSD post-hoc tests were carried out if there were significant factors or interactions in the repeated-measures ANOVA.

RESULTS

Water temperature and light were lower during the Autumn 3-month recovery period compared to both the Spring 3-month recovery period and the Autumn 10-month recovery period (Table 1). No light data was available for the Spring 10-month recovery period, however, the average temperature was intermediate compared to the other treatments (Table 1).

Recovery from 3-month light reduction treatments

Leaf biomass and density recovered (i.e. were not significantly different to controls) after 10 months re-exposure to ambient light (Figure 2), but not after 3 months, reflected in a significant

Recovery Period x Intensity interaction term (Table 2). Of particular interest was the response of the Spring treatments: the moderately shaded plots were not significantly different to the controls at the end of the light reduction period but after three months re-exposure to ambient light had declined, to be significantly lower than controls (Figure 2, Table 2). In contrast, the highly shaded treatment was lower than the controls after the shading period and showed an increase in leaf biomass and density after three months re-exposure to ambient light.

Cluster density in the Spring treatment showed a similar response to leaf biomass and density from the same time period (Figure 2, Table 2), but in the Autumn treatments the cluster density in the High treatment did not recover after 10 months re-exposure to ambient light, i.e. it was significantly lower than the control (Figure 2, Table 2). Stem biomass was not significantly impacted following light reduction in the Autumn treatments and all treatments had similar biomass during the recovery period (Figure 2, Table 2). However, in the Spring treatments, stem biomass in the high intensity plots was significantly lower than the controls or moderately shaded plots after 3 months of shading but had recovered to control conditions by three months re-exposure to ambient light (Table 2, Figure 2), reflected in the significant interaction terms (Table 2).

The response of algal epiphyte biomass to re-exposure to ambient light varied depending on the time that light reduction started (Table 2). In the Autumn treatments there was a significant interaction between intensity and recovery period: initial differences in biomass between the treatments and the controls were absent after 10 months due to a combination of increased biomass in the treatments and decline in biomass of the controls (Table 2, Figure 2). Contrasting this, in the Spring treatments there was no effect of light reduction treatment on algal epiphyte biomass, though biomass did tend to increase similarly in all three treatments over the recovery period.

Morphological and growth variables recovered faster than the biomass and density parameters. For the number of leaves per cluster and leaf extension there was a significant interaction between intensity and recovery period for both the Autumn and Spring samples (Table 2, Figure 3). After three months re-exposure to ambient light the number of leaves per cluster had returned

to control conditions in both time periods (Figure 3). The response of leaf extension rate varied depending on the time that the light reduction started (Table 2, Figure 3). In the Autumn treatments leaf extension rates were significantly higher than controls after 3 months re-exposure to ambient light, whilst in the Spring treatments leaf extension rates had not returned to control conditions, though they had increased. No data was collected from the recovery period of ten months. In all cases where leaf extension was observed, that growth occurred in all clusters after three months re-exposure to ambient light (Figure 3). Other morphological parameters such as leaf length, leaf width, stem internode length and canopy height were not significantly impacted by light reduction treatments and showed no difference to controls over the recovery period.

The physiological variables showed a variety of patterns with re-exposure to ambient light and were generally inconsistent between the two times, Autumn and Spring (Figure 4 and 5, Table 2). There was a significant interaction between intensity and recovery period for rhizome sugars in both the Autumn and Spring treatments (Figure 4, Table 2): at both times rhizome sugars were significantly reduced after three months of light reduction but recovered after three months exposure to ambient light. Rhizome starch also showed a significant interaction, but only in the Spring treatment where elevated concentrations dropped to control conditions after three months re-exposure to ambient light. There was no impact of shading on rhizome starch in the Autumn treatment or during the recovery period. Leaf soluble sugars also showed a significant interaction between intensity and recovery period that varied depending on the time: in the Autumn treatments, there was no significant effect of intensity at the end of the three month shading period, nor after three months re-exposure to ambient light, but after ten months re-exposure the moderate treatment had higher soluble sugars than the control and high treatment; in contrast, the Spring treatment recovered to control conditions within three months of re-exposure. There was no significant treatment effect on leaf starch in the Spring treatment, however, there was a significant interaction in the Autumn treatment. After three months light reduction there was no impact of intensity on leaf starch, but by three months the moderate intensity treatment was significantly lower than the control and after ten months re-exposure to ambient light both the moderate and high intensity treatments were significantly higher than the control (Table 2, Figure 3).

Leaf $\partial^{15}N$ showed a significant interaction between intensity and recovery period (Table 2, Figure 5), whereby values were significantly lower in the moderate and high treatments after three months of light reduction, but recovered to control conditions after three months re-exposure to ambient light. There was no significant treatment effect for rhizome $\partial^{15}N$ (Table 2, Figure 5). Leaf and rhizome nitrogen and leaf carbon had a significant interaction between intensity and recovery period but only in the Spring treatment. Elevated nitrogen levels and reduced carbon levels returned to control conditions after three months re-exposure to ambient light (Figure 5, Table 2). There was no impact or interaction of light reduction treatments on rhizome carbon and leaf and rhizome $\partial^{13}C$ (Table 2).

Recovery from 6 & 9-month PPFD reduction treatments

For plots shaded for six and nine months, there was no recovery of seagrass leaf and stem biomass or canopy height up to 23 months after the light reduction stress was removed and the meadow was re-exposed to ambient light (Table 2, Figure 6 and 7). In plots that had been shaded for 6 months starting in Autumn, leaf and stem biomass and canopy height declined further over the 23 months following removal of light reduction. The remaining stems were about half the height of those in the Control plots, around 30 cm high, and were new stem recruits or remnants of older stems. There were no further significant declines in algal epiphyte biomass (Table 2, Figure 6).

When shaded for 6 months starting in Spring, there were, again, further declines in stem biomass and canopy height, but not in leaf biomass (Table 2, Figure 6). Algal epiphyte biomass recovered to control levels 17 months after the light reduction impact but only in the moderate treatment; there was no change in the high treatment (Table 2, Figure 6).

In the plots shaded for nine months starting in Autumn and re-exposed to ambient light for 21 months, the pattern of change was similar to the Autumn six months impact treatments, with further declines in leaf and stem biomass and canopy height and no change in algal epiphyte biomass (Table 2, Figure 7). The Spring nine-month plots had a similar response to the Autumn nine-month plots, except there was a slight increase in the leaf biomass of the moderate

treatments, 15 months after the light reduction impact was removed, so that they were at an intermediate level between the control and high treatment (Table 2, Figure 7).

DISCUSSION

Approval for dredging activities in the marine environment in Australia requires predictions on the spatial and temporal extent of the physico-chemical change it will produce as well as the potential impact on the biota. Once approval is granted, monitoring is undertaken to assess these predictions and, at times, recovery (Bayer et al., 2008; Erftemeijer and Robin Lewis III, 2006). This study provides important new information to improve impact prediction for light reducing activities. It also provides information relevant to choosing potential indicators for recovery monitoring of *Amphibolis griffithii* seagrass throughout temperate Australia, though the concepts for benthic primary producer habitats are relevant world-wide.

Timescales of recovery

If light reduction to 5-18% of ambient light persists for a maximum of three months there is a significant impact to the *Amphibolis* seagrass habitat (up to 72% loss leaf biomass)(Lavery et al., 2009), but recovery of above-ground biomass can occur within the following 10 months. This has been demonstrated at two times of year, suggesting that recovery from that level of impact is not dependent on time of year. The recovery from three months of light reduction is faster than has previously been reported for larger seagrass species. Generally, recovery in these species takes years, decades or has been predicted to take centuries (Boese et al., 2009; Bryars and Neverauskas, 2004; Collier et al., 2009; Gonzalez-Correa et al., 2005; Hammerstrom et al., 2007; Neckles et al., 2005). Interestingly, this relatively fast recovery occurred despite up to 72% loss of leaf biomass, highlighting the fast leaf production rates of *Amphibolis* compared to other large seagrasses (Marba and Walker, 1999), and high recovery potential if actively growing clusters (up to 42%) remain on the stem from which new leaves can form. However, it should be noted that below-ground material, a significant component of these rhizomatous plants (~ 50% relative to the above-ground biomass (Lavery et al., 2009)) was not taken into account in assessing recovery. Di Carlo and Kenworthy (2008) found a general trend in larger seagrass species of faster aboveground than belowground recovery. So this recovery rate should be treated in the context

that it may be an underestimate of the entire seagrass components. It is also important to note that in these experiments the treatment plots were surrounded by healthy seagrass meadow, which could act as a source of recruitments of both stems and seedlings. Under typical light-reduction arising from dredging or eutrophication, the spatial scale of impact will be larger and this source of recruitment would be more distant, suggesting less potential for recovery than observed here.

Longer durations of light stress (6-9 months at 6-19% of ambient light) resulted in 82-100% loss of leaf biomass, and no recovery was detected in the 15- 23 months following removal of the light reduction stress. Consequently there is likely to be a threshold time between 3 and 6 months, regardless of light intensity. The experiment was concluded at this time so actual recovery times are not available for these longer duration dredging scenarios. This lack of recovery was comparable to other seagrass studies where recovery was shown or predicted to be slow (Gonzalez-Correa et al., 2005; Kendrick et al., 2000) or not detected (Kirkman, 1985; Walker et al., 2006). *A. griffithii* subjected to more severe stress had no or few surviving leaf clusters, thus recovery was mostly dependent on recruitment via production of new stems from existing rhizome or establishment of seedlings. Stem recruitment was observed but these stems did not persist. *A. griffithii* stores carbohydrate reserves in its rhizome which are known to decline during periods of shading (Lavery et al., 2009). It is likely that such reductions occurred here reducing carbohydrate reserves below the level required to support the actively growing new stems until they could develop sufficient photosynthetic tissue to be self-supporting. Seedlings were also observed but did not persist. There is little information on the survival rates of *A. griffithii* seedlings so it is not possible to comment on whether this lack of survival was unusual.

Recovery following severe impact will be slower than that following moderate impact as it depends on stem recruitment, which is slower than leaf production (Marba and Walker, 1999) (i.e. the plastochrone interval for stems is 259 days vs. 32 for leaves (Marba and Walker, 1999)) and seedlings are only produced for a few months during a year (Walker et al., 2001). Consequently, management of dredging or other light-reduction impacts should avoid stressing the seagrass to the point that recovery is required through recruitment of new stems or seedlings.

We are unable to conclude whether these meadows will eventually recover, though we cannot discount that possibility. If recovery does occur, it will be slow and, consequently the loss of ecological function would occur over a longer timescale.

Process of recovery

The pathway of recovery in the plants that had been shaded for 3 months, commenced with an increase in the major carbohydrate stores (sugars in the rhizome and leaves) back to control conditions and a return to an average of three leaves cluster^{-1} within three months of re-exposure to ambient light. This indicates that the plants were actively increasing leaves to maximise their ability to capture light, and the product of this, carbohydrates were accumulating in the plant. In all cases, leaves within leaf clusters grew but the rate varied depending on the time of year. The variability in the growth rate response indicates that the rate of recovery of some ecological functions will depend on the time of year that impacts occur and cease. In this case, plants shaded over autumn and recovering over winter achieved leaf extension rates comparable to controls within 3 months, while those shaded over spring and recovering during summer did not reach control growth rates. This reflects differences in the rate of growth of control plants rather than differences in the growth rate of the plants subjected to shading. That is, irrespective of time of year that plants were shaded, they demonstrated a similar capacity to recover from shading but because plants recovering over summer are compared to controls at a time when higher temperature and PPFD allow high control growth rates, they failed to equal those rates and consequently were deemed to have not recovered. This clearly has implications for the assessment of recovery in management programmes depending on how recovery is defined

The $\delta^{15}N$ of leaves returned to control values within 3 months of re-exposure to ambient light. Lavery et al (2009) proposed that the change in $\delta^{15}N$ with light reduction were due to changes in the allocation of nitrogen between light harvesting pigments (depleted in ^{15}N relative to bulk ^{15}N of cells) and electron carriers and Calvin cycle enzymes (enriched in ^{15}N relative to bulk ^{15}N of cells) (Evans, 1989; Evans and Poorter, 2001; Werner and Schmidt, 2002). The elevation in $\delta^{15}N$ on the return to ambient light levels is consistent with the plants investing the nitrogen resources in electron carriers and Calvin cycle enzymes rather than light harvesting pigments. This further

supports the earlier suggestion (Lavery et al., 2009) that $\delta^{15}N$ may be a useful indicator of altered light availability that will respond earlier than the morphological changes that mangers are often seeking to avoid.

Leaf biomass and density of the meadow were the next features of the meadow to recover, however, the trajectory of recovery varied depending on time of year and type of light reduction treatment. There was an increase in leaf biomass and density in the first three months when conditions were more conducive for growth, water temperatures were higher and light was higher. For example in plots where the light stress was removed in winter, there was no significant change in leaf biomass and density three months into the recovery period (June-Oct, 19°C, 6-16 mol m^{-2} d^{-1}), but in the plots where the light stress was removed in summer, the leaf biomass and density in the high intensity treatments only, started to recover over the first three months (Dec-March, 19-21°C, 42-49 mol m^{-2} d^{-1}). This trajectory of recovery observed in the first three months over summer and autumn may reflect the environmental conditions at the time of the recovery period but also the internal growth patterns of the plants. Yet, our data do not show faster growth rates of recovering plants at different times of year. Although control growth rates as measured by the leaf extension were higher in autumn (1.4 ± 0.02 mm $cluster^{-1}$ d^{-1}) compared to spring (0.8 ± 0.04 mm $cluster^{-1}$ d^{-1}), there was no difference in the growth rate of recovering plants at different times of year growth (1 mm $cluster^{-1}$ d^{-1}, Figure 2). There may have been differences in growth earlier on in the recovery period, only the last two weeks were measured in this study, and leaf production rates are known to be higher in summer than winter (Carruthers, 1999; Walker and Cambridge, 1995) potentially accounting for more leaf production and increases in leaf density at this time. These points highlight again how single indicators of recovery may be misleading and that a combination of morphological and physiological indicators may provide a better appreciation of the state of the seagrass at different times of year.

One of the most surprising results was the decline in leaf biomass of one treatment following removal of shading despite showing no significant difference from the controls at the end of the 3-month shading period. This highlights the potential variability in response once a light

reduction stress has been removed. Other light reduction studies have also observed this (Malta et al., 2006), though the mechanism for this reduction is not clear. A possible explanation is that the sudden increase in light following removal of shading (7.4 to 41.6 mol m^{-2} d^{-1}, Table 1) may cause photo-oxidative damage to previously dark-adapted plant tissue. Irrespective of the mechanism, the result, and its observation in other studies, indicates that recovery from shading should not be presumed following the removal of shading, even if plants have shown no morphological response during the shading period. Impacts may occur following the removal of stress and this needs to be factored into the predications of, and monitoring for impacts.

The algal epiphyte biomass was not impacted in the treatments shaded at the end of winter. This contradicts the general theory that algae responds faster to light reduction than seagrasses. But in the plots shaded at the end of summer there was recovery after three months in the moderate treatment, and 10 months in the high intensity treatment. In this scenario algal biomass recovered faster than seagrass leaf biomass, but only in the moderately shaded plots. Within *Amphibolis* seagrass meadows the amount of algal epiphytes is generally greater than other large seagrass species, and highly variable seasonally and over small spatial scales (10's of meters) (Lavery and Vanderklift, 2002). Therefore within this species algal biomass may not be a reliable indicator of impact to and recovery from light stress.

MANAGEMENT IMPLICATIONS

There are three main management outcomes from this research. Firstly, an improved capacity for predicting impacts of light reduction in *Amphibolis* seagrass meadows. We know that recovery can occur within a year, following light reduction for durations of up to 3 months, with relatively high amounts of light reduction (82-95%). This recovery is facilitated by rapid leaf production, and such short timescales have rarely been reported for large seagrass. To ensure that this speed of recovery occurs actively growing clusters, at least 42% relative to control numbers must remain on the vertical stem.

It is important to note that this study has examined the recovery of the seagrass *Amphibolis griffithii* from light reduction stress, where this stress was imposed to mimic the duration and

intensity of turbid plumes generated from dredging operations. It has not incorporated the potential stress associated with sedimentation from turbid plumes. It is likely that impacts observed in this study would be more severe with the added stress of sedimentation, and as a consequence recovery would be longer.

Longer durations of light reduction (6-9 months) at similar intensities (82-95%) result in much longer timescales of recovery, definitely greater than 2 years. Observations on the recovery of seagrasses from a dredging operation support these experimental findings that recovery will take longer than 2 years. Before this study began, a real-life dredging operation created a turbid plume ~ 70 km along the coast, and 1-2 km out to sea for around 9 months (Mulligan, 2005). There were extensive declines in *Amphibolis* seagrass cover (72-100%) up to 5 km away from the dredging operation (CSIRO, 2007). Around four sites containing *Amphibolis* were monitored for three years after the dredging operation was completed. There was some recovery at all of these sites after three years (33-68% relative to pre-dredging conditions) but the meadows had not retuned to the cover that was present before the dredging operation began (CSIRO, 2007).

Secondly, despite no observable effects on leaf biomass detected at the end light reduction phase, there can be subsequent declines during the recovery phase. Therefore, it is imperative to monitor the biological components of the ecosystem once the stress is removed to ascertain if there have been any biological impacts.

Thirdly, there are five potential indicators of recovery in the meadow. These have been selected based on their sensitivity such as speed of response and consistency at different times of the year and with different intensities of stress. They are suitable for a scenario where recovery is expected within a year, but may not be appropriated in situations where there has been a more severe disturbance and the majority of the leaf biomass has been lost. The potential indicators presented here are a subset of the sub-lethal light stress indicators identified by Lavery et al (2009). Three potential indicators responded after 3 months re-exposure to ambient light, rhizome sugars, average leaves cluster^{-1} and the $\delta^{15}N$ signal of leaves. The remaining two potential recovery indicators are leaf biomass and density, which indicate a condition further along the recovery pathway.

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LEGENDS

Table 1: Water temperature and light in the different recovery treatments.

Table 2: Results of statistical analysis to determine the effect of intensity over the recovery period on the 3-, 6- and 9-month light reduction treatments for *A. griffithii* seagrass meadow biomass, density, morphology and physiology variables. *** = $p < 0.001$, ** = $p < 0.01$ & > 0.001, * = $p < 0.05$ & > 0.01.

Figure 1: Schematic diagram of the timing of treatments for different start-times and durations in the impact phase (grey) and recovery phase (white bars). Samples were collected at the time associated with the end of each bar, i.e. 3 times in the 3-month durations and 2 times in the 6- and 9-month durations. In the 3-month treatments there were 2 recovery duration sampling events, at 3 (3R) and 10 (10R) months.

Figure 2: Biomass (g DW m^{-2}) and density (m^{-2}) of *A. griffithii* and biomass (g DW m^{-2}) of algal epiphytes following recovery from 3-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control, Moderate, High factors. Letters indicate significant differences between PPFD reduction treatments (Intensity) at a particular Time and Recovery period. Average with standard error bars.

Figure 3: Morphology and growth measures of *A. griffithii* following recovery from 3-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control, Moderate, High factors. Letters indicate significant differences between PPFD reduction treatments (Intensity) at a particular Time and Recovery period. Average with standard error bars. nd indicates no data for that duration.

Figure 4: Carbohydrate content (% DW) of *A. griffithii* following recovery from 3-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control, Moderate, High factors. Letters indicate significant differences between PPFD reduction treatments (Intensity) at a particular Time and Recovery period. Average with standard error bars.

Figure 5: Nutrient content (% DW) and nitrogen stable isotope values of *A. griffithii* plant parts following recovery from 3-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control, Moderate, High factors. Letters indicate significant differences between PPFD reduction treatments (Intensity) at a particular Timing and Recovery period. Average with standard error bars.

Figure 6: Biomass (g DW m^{-2}), density and morphology of *A. griffithii* following recovery from 6-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control,

Moderate, High factors. The length of the Recovery period varies with treatment. Average with standard error bars.

Figure 7: Biomass (g DW m^{-2}), density and morphology of *A. griffithii* following recovery from 9-months of PPFD reduction treatments with Timing: Autumn, Spring and Intensity: Control, Moderate, High factors. The length of the Recovery period varies with treatment. Average with standard error bars.

TABLES

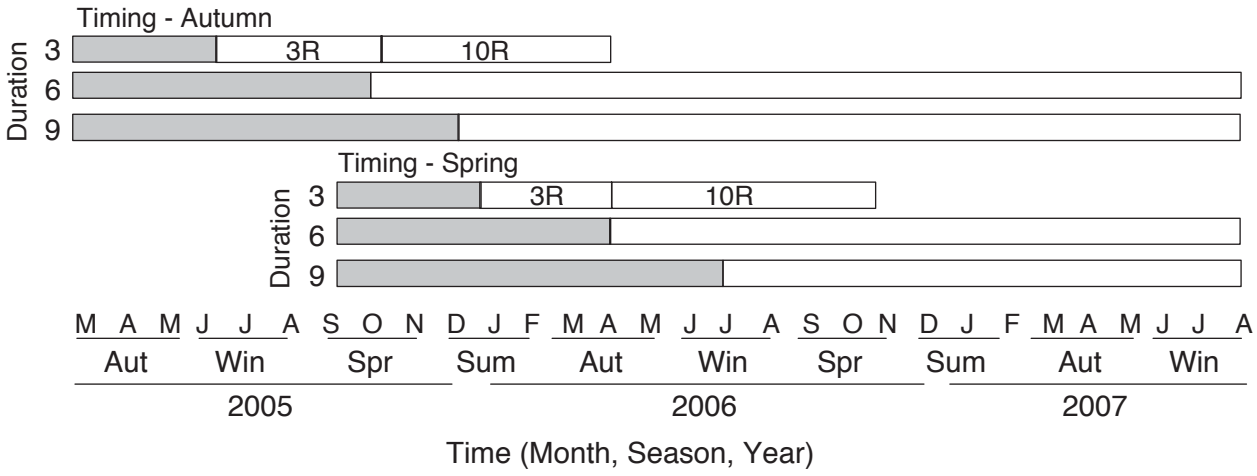
Table 1

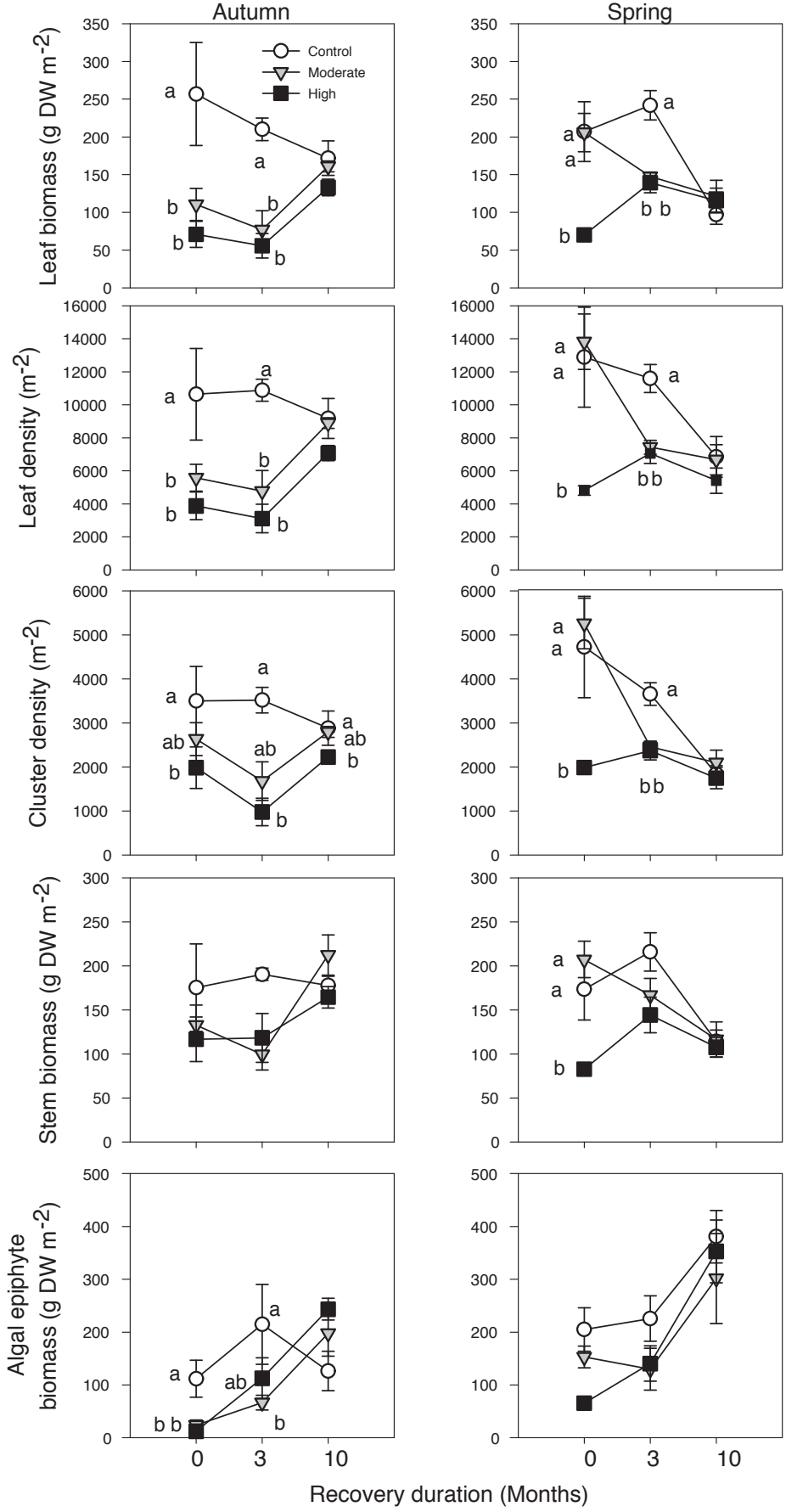
	Water temp. (ºC)	Avg. total daily irradiance (mol m^{-2} d^{-1})	Avg. H_{SAT} (hrs)		Water tp. (ºC)	Avg. total daily irradiance (mol m^{-2} d^{-1})	Avg. H_{SAT} (hrs)
Autumn				Spring			
3-month	21.7 (19-22)			3-month	18.7(18-19)		
Control		19.0	9.52	Control		41.6	12.20
Moderate		3.1	4.31	Moderate		7.4	7.13
High		0.9	1.17	High		4.7	3.18
Recovery 3	18.4 (18-19)	16.1	9.48	Recovery 3	20.5 (19-22)	41.1	12.15
Recovery 10	20 (18-21)	41.2	12.1	Recovery 10	19.1 (18-20)	nd	nd
6-month	20 (18-22)			6-month	19.9(18-22)		
Control		16.6	9.34	Control		41.3	12.13
Moderate		2.8	3.62	Moderate		5.8	7.14
High		1.0	1.53	High		3.5	3.27
9-month	19.6 (18-22)			9-month	19.8 (18-22)		
Control		25.4	10.09	Control		32.2	11.36
Moderate		4.8	4.90	Moderate		4.3	6.37
High		2.4	2.12	High		2.7	2.84

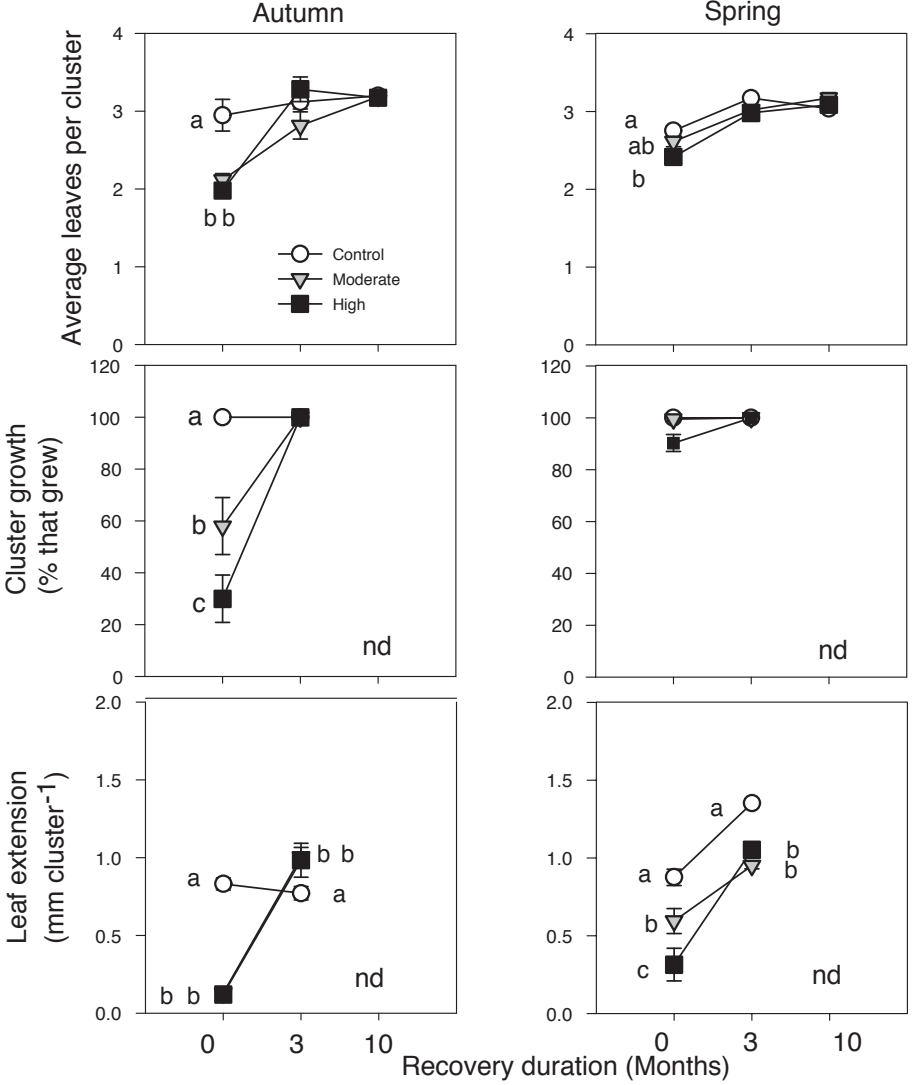
Table 2:

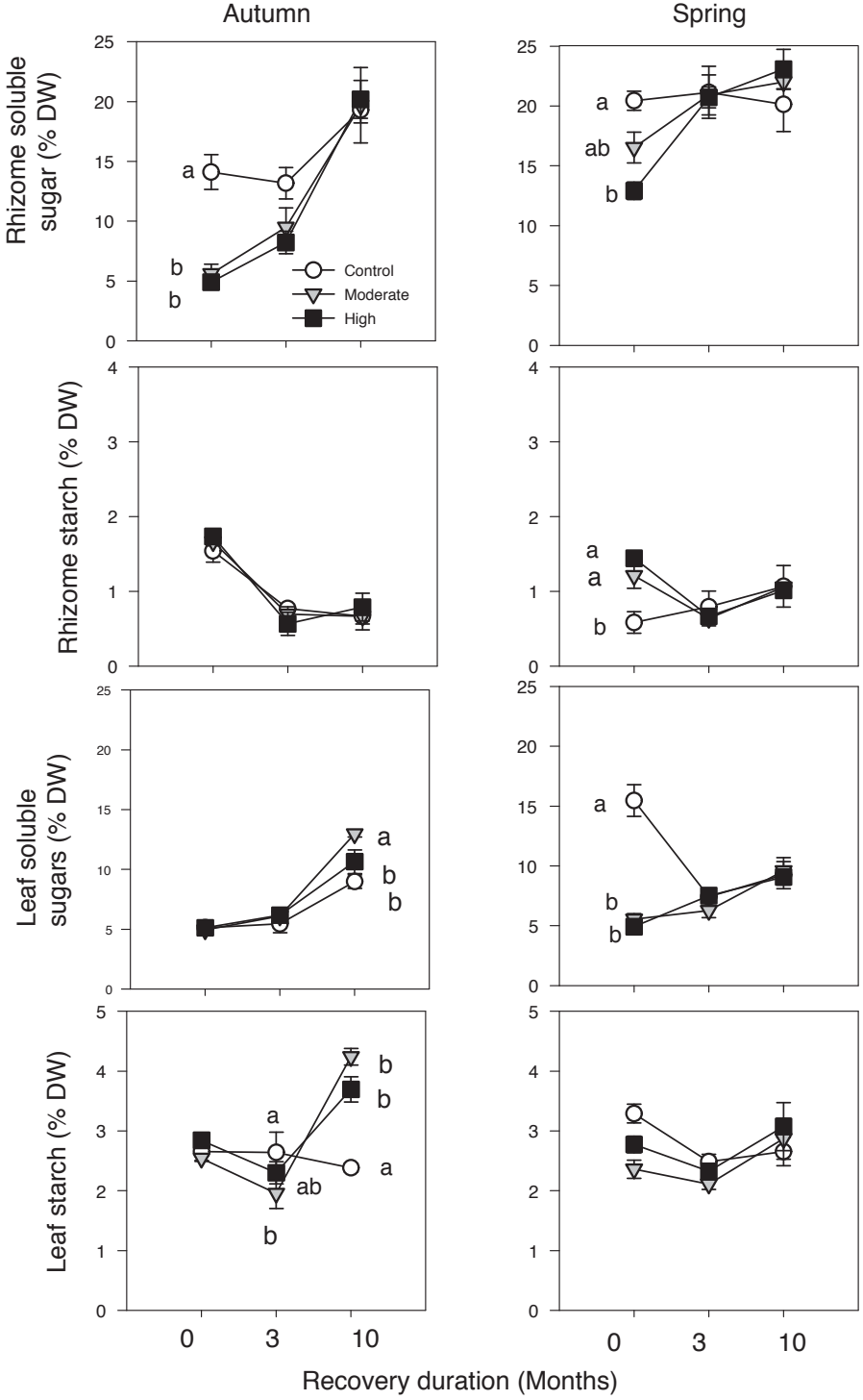
	Autumn			Spring			Autumn			Spring			Autumn			Spring			Autumn			Spring		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
3-month duration treatments																								
	Leaf Biomass $_{Ln}$ (g DW m^{-2})						Stem biomass (g DW m^{-2})						Algal epiphyte biomass $_{Sqrt}$ (g DW m^{-2})						Leaf density $_{Ln}$ (m^{-2})					
Intensity (I)	2	15.3	***	2	6.63	*	2	2.49	0.12	2	4.66	*	2	2.24	0.15	2	3.49	0.06	2	16.9	***	2	8.02	**
Recovery (R)	2	6.32	**	2	10.2	**	2	3.85	*	2	10.7	***	2	21.4	***	2	15.4	***	2	5.38	*	2	9.65	**
R x I	4	3.48	*	4	8.14	***	4	1.83	0.16	4	4.45	**	4	5.61	**	4	0.6	0.67	4	2.60	0.06	4	5.24	**
	Cluster density (m^{-2})						Average leaves per cluster						80th percentile canopy height (cm)						Average leaf length (mm)					
Intensity (I)	2	12.6	**	2	6.76	*	2	6.32	*	2	4.8	*	2	2.25	0.15	2	0.39	0.68	2	6.24	**	2	2.57	0.12
Recovery (R)	2	2.09	0.14	2	23.0	***	2	56.4	***	2	126	***	2	3.20	0.06	2	12.7	***	2	25.6	***	2	0.77	0.47
R x I	4	1.53	0.22	4	5.44	**	4	9.72	***	4	6.30	**	4	0.25	0.91	4	2.28	0.09	4	2.46	0.07	4	1.15	0.36
	Average leaf width (mm)						Average internode length (mm)						Leaf extension (mm cluster^{-1} day^{-1})						Rhizome sugars (% DW)					
Intensity (I)	2	1.49	0.26	2	0.49	0.62	2	2.55	0.12	2	0.12	0.89	2	10.1	**	2	29.8	***	2	6.33	*	2	1.15	0.35
Recovery (R)	2	9.22	**	2	1.45	0.26	2	2.13	0.14	2	3.98	*	1	146	***	1	109	***	2	51.3	***	2	9.75	**
R x I	4	5.74	**	4	1.43	0.25	4	2.51	0.07	4	1.64	0.20	2	44.6	***	2	5.10	*	4	3.49	*	4	3.09	*
	Rhizome starch (% DW)						Leaf sugars (% DW)						Leaf starch (% DW)						Leaf nitrogen (% DW)					
Intensity (I)	2	0.11	0.89	2	1.26	0.32	2	4.10	*	2	20.0	***	2	6.66	*	2	1.53	0.26	2	1.12	0.36	2	18.4	***
Recovery (R)	2	48.5	***	2	7.90	**	2	131	***	2	8.18	**	2	24.2	***	2	7.81	**	2	73.3	***	2	6.51	**
R x I	4	0.65	0.63	4	4.93	**	4	5.60	**	4	18.5	***	4	10.9	***	4	2.59	0.06	4	0.94	0.46	4	15.5	***
	Rhizome nitrogen (% DW)						Leaf ∂^{15}N						Rhizome ∂^{15}N						Leaf carbon (% DW)					
Intensity (I)	2	0.84	0.45	2	1.57	0.25	2	2.85	0.10	2	3.49	0.06	2	5.53	*	2	0.26	0.77	2	0.77	0.48	2	0.42	0.66
Recovery (R)	2	49.9	***	2	8.60	**	2	23.1	***	2	0.75	0.48	2	1.43	0.26	2	13.0	***	2	1.72	0.20	2	12.5	***
R x I	4	1.17	0.35	4	8.32	***	4	5.31	*	4	6.03	**	4	2.25	0.09	4	1.92	0.14	4	1.80	0.16	4	3.16	*
	Rhizome carbon (% DW)						Leaf ∂^{13}C						Rhizome ∂^{13}C											
Intensity (I)	2	1.40	0.28	2	0.59	0.57	2	1.26	0.32	2	0.36	0.70	2	0.37	0.70	2	0.52	0.61						
Recovery (R)	2	7.26	**	2	13.4	***	2	11.1	***	2	3.95	*	2	2.47	0.11	2	0.17	0.84						
R x I	4	1.88	0.15	4	0.50	0.74	4	0.94	0.46	4	0.79	0.54	4	0.74	0.57	4	2.30	0.09						
6-month duration treatments																								
	Leaf Biomass $_{Ln}$ (g DW m^{-2})						Stem biomass $_{Ln}$ (g DW m^{-2})						Algal epiphyte biomass $_{Ln}$ (gDW m^{-2})						80th percentile canopy height (cm)					
Intensity (I)	2	121	**	2	194	***	2	48.8	**	2	19.3	***	2	87.0	**	2	29.5	***	2	59.0	***	2	37.5	***
Recovery (R)	1	86.5	**	1	3.40	0.09	1	106	**	1	36.6	***	1	2.73	0.12	1	4.69	0.05	1	81.7	***	1	116	***
R x I	2	5.30	0.02	2	3.80	0.05	2	21.7	**	2	0.74	0.50	2	1.05	0.38	2	6.49	*	2	9.28	**	2	30.4	***
9-month duration treatments																								
	Leaf Biomass $_{Ln}$ (g DW m^{-2})						Stem biomass $_{Ln}$ (g DW m^{-2})						Algal epiphyte biomass $_{Ln}$ (gDW m^{-2})						80th percentile canopy height (cm)					
Intensity (I)	2	249	**	2	38.5	***	2	47.1	***	2	19.8	***	2	40.8	***	2	12.7	**	2	19.6	***	2	53.1	***
Recovery (R)	1	0.50	0.49	1	1.11	0.31	1	117	***	1	60.4	***	1	2.14	0.17	1	0.71	0.42	1	72.8	***	1	130	***
R x I	2	9.80	*	2	7.55	*	2	24.5	***	2	5.78	*	2	2.86	0.10	2	1.4	0.28	2	9.68	***	2	25.9	***

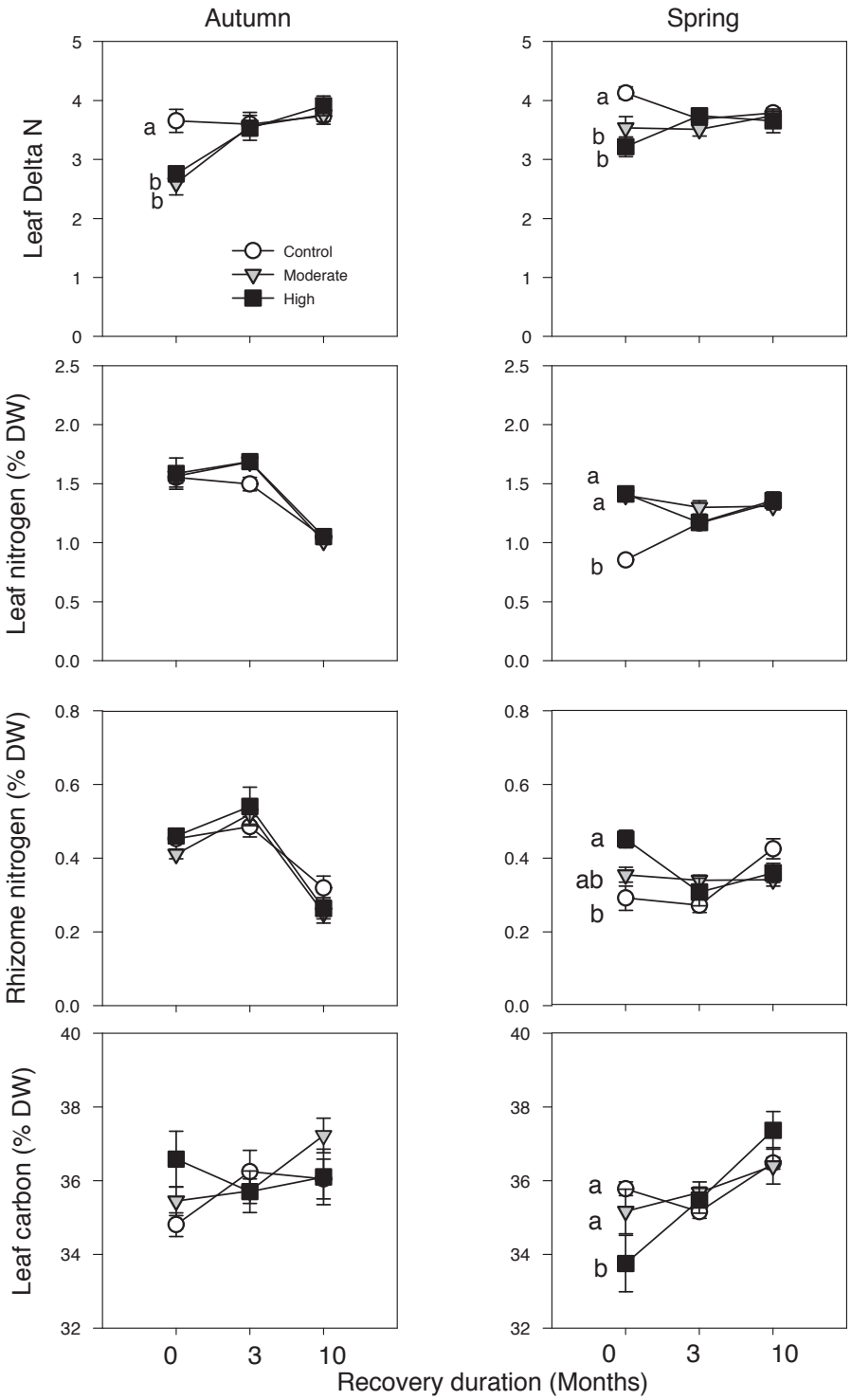
Sqrt – Square root transformed, Ln – Natural log transformed

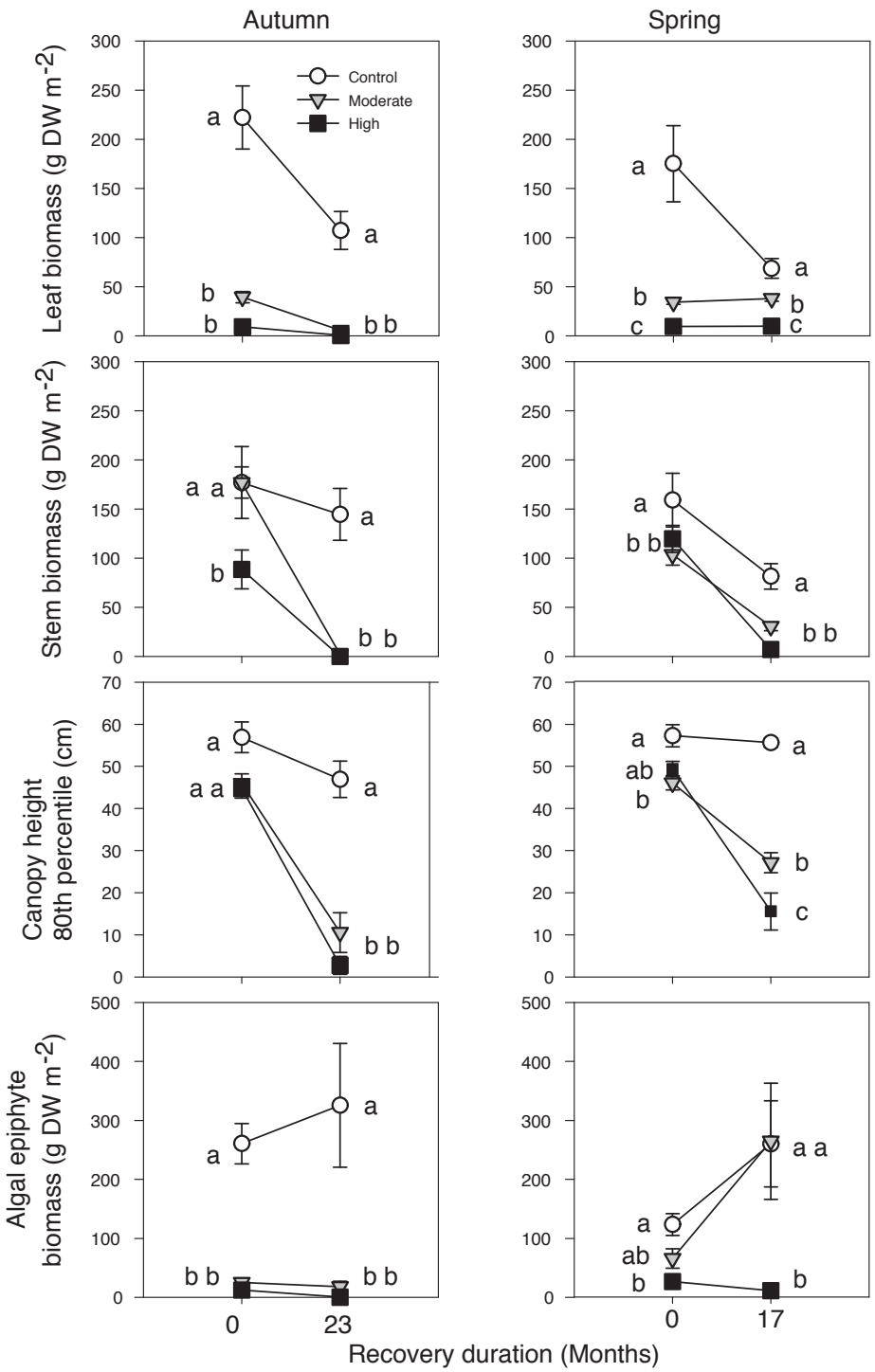

Timing - Autumn
Duration
3
6
9
3R
10R
Timing - Spring
Duration
3
6
9
3R
10R
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
Aut Win Spr Sum Aut Win Spr Sum Aut Win
2005 2006 2007
Time (Month, Season, Year)

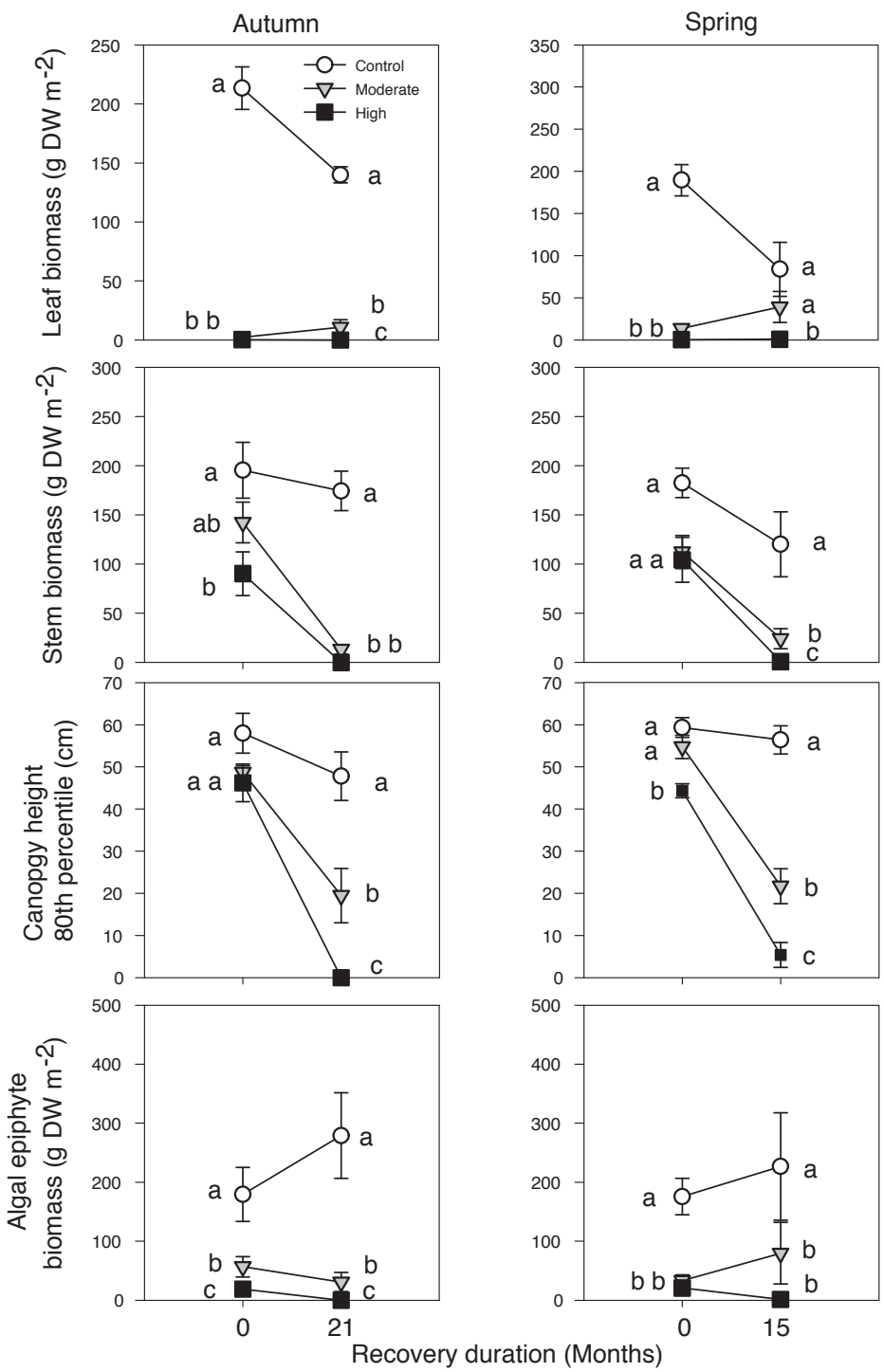

Autumn
Spring
Control
Moderate
High
Leaf biomass (g DW m-2)
Leaf density (m-2)
Cluster density (m-2)
Stem biomass (g DW m-2)
Algal epiphyte biomass (g DW m-2)
Recovery duration (Months)
0
3
10


Autumn
Spring
Average leaves per cluster
Control
Moderate
High
a
b b
a
ab
b
Cluster growth
(% that grew)
a
b
c
nd
nd
Leaf extension
(mm cluster-1)
a
b b
a
b b
a
b
c
b
b
nd
nd
0
3
10
Recovery duration (Months)


Autumn
Spring
Rhizome soluble sugar (% DW)
Rhizome starch (% DW)
Leaf soluble sugars (% DW)
Leaf starch (% DW)
Control
Moderate
High
Recovery duration (Months)


Autumn
Spring
Leaf Delta N
Leaf nitrogen (% DW)
Rhizome nitrogen (% DW)
Leaf carbon (% DW)
Control
Moderate
High
a
b
b
a
b
b
a
a
b
a
ab
b
a
a
b
0
3
10
Recovery duration (Months)


Autumn
Spring
Control
Moderate
High
Leaf biomass (g DW m-2)
Stem biomass (g DW m-2)
Canopy height 80th percentile (cm)
Algal epiphyte biomass (g DW m-2)
Recovery duration (Months)
0
23
17


Autumn
Spring
Control
Moderate
High
Leaf biomass (g DW m-2)
Stem biomass (g DW m-2)
Canopgy height
80th percentile (cm)
Algal epiphyte
biomass (g DW m-2)
Recovery duration (Months)
0
21
15