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Recovery mechanisms: understanding mechanisms of seagrass recovery following disturbance

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WAMSI Dredging Science Node

Report

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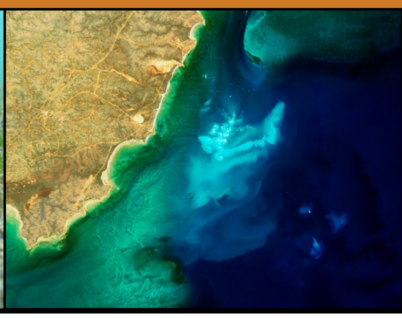


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WAMSI Dredging Science Node

The WAMSI Dredging Science Node is a strategic research initiative that evolved in response to uncertainties in the environmental impact assessment and management of large-scale dredging operations and coastal infrastructure developments. Its goal is to enhance capacity within government and the private sector to predict and manage the environmental impacts of dredging in Western Australia, delivered through a combination of reviews, field studies, laboratory experimentation, relationship testing and development of standardised protocols and guidance for impact prediction, monitoring and management.

Funding Sources

The $20million Dredging Science Node is delivering one of the largest single issue environmental research programs in Australia. This applied research is funded by **Woodside Energy, Chevron Australia, BHP Billiton and the WAMSI Partners** and designed to provide a significant and meaningful improvement in the certainty around the effects, and management, of dredging operations in Western Australia. Although focussed on port and coastal development in Western Australia, the outputs will also be broadly applicable across Australia and globally.

This remarkable **collaboration between industry, government and research** extends beyond the classical funder-provider model. End-users of science in regulator and conservation agencies, and consultant and industry groups are actively involved in the governance of the node, to ensure ongoing focus on applicable science and converting the outputs into fit-for-purpose and usable products. The governance structure includes clear delineation between end-user focussed scoping and the arms-length research activity to ensure it is independent, unbiased and defensible.

And critically, the trusted across-sector collaboration developed through the WAMSI model has allowed the sharing of hundreds of millions of dollars worth of environmental monitoring data, much of it collected by environmental consultants on behalf of industry. By providing access to this usually **confidential data,** the **Industry Partners** are substantially enhancing WAMSI researchers' ability to determine the real-world impacts of dredging projects, and how they can best be managed. Rio Tinto's voluntary data contribution is particularly noteworthy, as it is not one of the funding contributors to the Node.

Funding and critical data **Critical data**

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Front cover images (L-R)

Image 1: Trailing Suction Hopper Dredge *Gateway* in operation during the Fremantle Port Inner Harbour and Channel Deepening Project. (Source: OEPA)

Image 2: *Halophila ovalis* meadow at Thevenard Is, Pilbara Region. (Source: Kathryn McMahon, ECU)

Image 3: Dredge plume at Barrow Island. Image produced with data from the Japan Aerospace Exploration Agency (JAXA) Advanced Land Observing Satellite (ALOS) taken on 29 August 2010.

Image 4: WAMSI Scientist monitoring recovery of seagrass from cleared experimental plots. (Source: Paul Lavery, ECU)

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Executive Summary

Although seagrasses are sensitive to natural and anthropogenic disturbances, many species have the capacity to recover from disturbance within relatively short time frames. In tropical regions, such as the north west of Western Australia, small-leaved species of seagrasses are often characterised by natural patterns of loss and recovery over time periods spanning months or longer. Studies have consistently found that vegetative growth (extension of rhizomes of remaining plants) accounts for most recovery, though recovery from seeds has also been recorded. Understanding which of these mechanisms dominates at a particular location is important for predicting the potential for seagrass recovery following loss or reduction in abundance due to anthropogenic disturbance, such as from dredging-related pressures.

The objective of this project was to examine the capacity, duration and mechanisms of recovery of seagrass from a severe localised disturbance, and in particular, whether seagrass recovery is by vegetative regrowth from rhizome extension (i.e. asexual) or via recruitment from seeds (i.e. sexual). To address this, a long-term, field-based, manipulative, seagrass clearance and recovery experiment was conducted at Thevenard Island (21.5°S, 115.0°E). The experiment commenced in November 2014 in seagrass meadows at two water depths, a 'Shallow' site (2 m) and 'Deep' site (6 m). At each site the same experimental design was used. This involved removing seagrass from circular plots (75 cm diameter) and comparing the recovery in plots where lateral extension of rhizomes was prevented by a physical barrier (i.e. a plastic border sunk into the sediment to a depth of 6 cm to prevent rhizome extension from surrounding meadow) with plots in which no barrier was present.

Changes in seagrass cover were examined in all treatments after 8, 21, 59, 104 and 208 days. The experiment was interrupted by Tropical Cyclone Olwyn (March 2015), which passed close to the study site between the last 2 survey dates, dramatically reducing seagrass cover at both sites, and removing the experimental enclosures at the Shallow site. Nevertheless, the survey results up to that point showed very clear evidence of recovery in cleared plots without barriers.

At the Shallow site, by 59 days, cleared plots without barriers contained significantly more seagrass cover than plots with barriers, and was comparable to undisturbed control plots. In contrast, the cleared plots with barriers (and which therefore depend on recovery from either seeds or fragments washing into the plot rather than growth from the surrounding meadow) did not contain seagrass on any of the survey dates during the experiment. During the experiment prior to the passage of Tropical Cyclone Olwyn (i.e. by 104 days), there was almost full recovery of the cleared plots in which vegetative growth could occur, but no recovery where this required recovery from seed or immigration of plant fragments.

At the Deep site, cleared plots with no barriers again showed a recovery of cover to levels comparable to the controls by 59 days, while cleared plots with barriers never contained any seagrass — a result that was consistent with the patterns observed at the shallow site. At both sites, maps of the location of seagrass within cleared plots showed that, where recovery occurred, it started at the edges of plots and then increased towards the centres of plots during the experiment.

These results indicate that the primary mechanism for recovery of seagrass (primarily *Halophila ovalis*) at Thevenard Island was through vegetative regrowth, and that the length of time it took for ~0.5 m^2 cleared patches to fully recover was 2 to 3 months. The most abundant species of seagrass present at Thevenard Island (*H. ovalis*) is also the most widespread species found in the Pilbara, and the photosynthetic flux densities and sediment grain sizes were within the ranges measured elsewhere in the Pilbara, so we predict that recovery elsewhere should follow similar patterns. Recovery from disturbances that remove seagrass from relatively small areas should occur within months, provided that sufficient meadow remains for rhizomes to colonise from (our clearances were ~0.5 m^2). However, in situations where seagrass loss occurs over a larger area, recovery might

rely more heavily on immigration of plant fragments or seeds from distant sites, which will take much longer. At this stage we have insufficient data to predict the time required for recovery in such situations.

Considerations for predicting and managing the impacts of dredging

In Western Australia, predicting and managing the impacts of dredging is guided by the *Technical Guidance: Environmental Impact Assessment of Marine Dredging Proposals* (EPA 2016). The same framework is applied, in modified forms, elsewhere in Australia. The framework has three phases which can benefit from the input of new information on biological components of marine ecosystems:

- a pre-development phase, which includes surveys and investigations to define the system in which dredging might occur;
- an impact assessment phase, in which the potential dredging-generated pressure fields and their effect on sensitive components of the environment need to be predicted, and monitoring undertaken; and
- a post-assessment verification of the impacts and gathering of reference data.

Below, we consider the implications of the findings of this project in the context of the various phases of the framework contained in EPA (2016).

Pre-development Surveys

Episodic events, such as Tropical Cyclone Olwyn, which occurred during this project, can completely remove seagrass meadows. While this has long been suspected, this study documented the potential severity of such events (causing total seagrass cover in control plots at the shallow site to drop from 25 to 30%, to 0%) and showed that seagrass may be absent from a site several months after a cyclone (seagrass was absent on 10 June 2015, 92 days after Tropical Cyclone Olwyn). Shallow meadows are likely to be more affected by cyclones than deep meadows, as evidenced by the presence of a small amount of seagrass at the Deep site in June 2015. It is likely that the colonising species of seagrass that we have studied in the Pilbara can recover from episodic disturbance and companion studies (see WAMSI DSN Project 5.3; Vanderklift et al. 2017) indicate that *H. ovalis* meadows in the Pilbara often have a phenology with strong meadow growth during the spring–summer period each year. These observations indicate that:

- **pre-development surveys should take into account previous cyclone activity** at potential survey sites to maximise the likelihood of observing seagrass. The probability of observing seagrass in surveys will be increased by avoiding cyclone-affected areas as it remains unclear how long it takes for seagrass to recover following cyclone damage. If there is no option but to use cyclone-affected areas, then repeat surveys over several years may be required in order to detect seagrass; and

- for general surveys of areas to determine seagrass presence, the inclusion of a range of water depths may increase the probability of encountering seagrasses, since deep sites might be more able to resist cyclone or other hydrodynamic-related disturbances. However, where surveys are designed to identify appropriate reference sites, an over-riding imperative would be to match water depth and other site characteristics to that of the dredging monitoring site.

Impact Assessment

While the transferability of inferences from this study to other places in the Pilbara is somewhat hampered by the substantial variation in abundance and species composition from place to place, the main species of seagrass present at the sites used in this study (*H. ovalis*) is widespread throughout the north west of Western Australia. Therefore, the findings will likely have relevance to most sites in the Pilbara that might be affected by dredging. The nature of the experimental disturbance (removal of all seagrass, including roots and rhizomes) is a reasonable facsimile of a severe dredging-induced disturbance, though the spatial extent of the experimental clearances (~0.5 m^2) is orders of magnitude smaller than the spatial extent of seagrass loss that has been reported following dredging events (see Erftemeijer & Lewis 2006). With this in mind, the implications of the study for impact prediction need to take into account the spatial scale of the predicted impact:

- damage at relatively small spatial scales, typical of that due to anchoring of vessels and deployment of equipment, is likely to be temporary in meadows comprised of small-leaved species, such as *Halophila* spp. This is consistent with the nature of these seagrasses and their ability to recover from natural pressures. These species of seagrass occur in areas that experience episodic natural disturbances (such as cyclones). Their survival depends on being able to resist or recover from these disturbances. Our findings indicate that a primary mechanism for recovery is through extension of vegetative growth from surrounding meadow(s) into disturbed patches. **If an impacted area is relatively small (our clearances were ~0.5 m^2, but we predict similar results for clearances up to tens of m^2 in extent) and surrounded by otherwise unaffected meadow, significant regrowth could be expected within a period spanning up to a few months;**

- while it is plausible that recovery through rhizome extension is easily achieved for unvegetated patches within meadows, this is less likely for disturbance at the scale of hectares. Collectively, the results from this project, WAMSI DSN Projects 5.2 (Seagrass Genetics; McMahon et al 2017a) and 5.3 (Natural Dynamics; Vanderklift et al. 2017) indicate that **although there can be short-term recovery (less than 1 year) from seed banks, this cannot be assumed**, even at sites where sexual reproduction is considered important for maintaining the seagrass population; and

- the clear evidence of rapid recovery from vegetative growth coupled with the lack of evidence of recovery from seed suggests that **managing for the retention of some vegetative material will increase the rate of recovery following dredging**. Complete loss of all vegetation will result in longer periods required for recovery.

Post-Assessment

While not directly related to this project of the DSN, there are a number of agent-based modelling approaches, which are commonly used to predict the re-growth of seagrass meadows (e.g. Kendrick et al. 2005). These models require input of the seagrass growth rates and branching patterns and may prove useful in estimating the recovery time of meadows based on vegetative growth. The data in this study on recovery rates can provide a calibration or validation data set for such models focused on *H. ovalis* in the Pilbara region.

Residual Knowledge Gaps

This project has significantly increased our understanding of the mechanisms by which seagrasses in the north west of Western Australia recover following disturbance, but it has also highlighted a number of enduring knowledge gaps.

Recovery from seed

The relative importance of seeds in post-disturbance recovery of seagrass meadows in the north west of Western Australia after disturbance remains unresolved. The difficulty in obtaining seed from sediments at the study site meant that we could not manipulate the density of seeds in our experiment. Consequently, the strength of our inferences about the role of seeds is weaker than it is for vegetative re-growth. Improved understanding would arise from studies that can quantify the rate of seed production, and the fate of seeds produced (including consumption by seed predators). In addition, experiments quantifying rates of recovery in places and situations where a viable seedbank is present would help refine knowledge of how important this mechanism is for recovery from disturbance.

Recovery following large-scale disturbance

The spatial scale of our disturbance experiment was necessarily small (~0.5 m^2) relative to the spatial extent of pressure fields generated by dredging. The mechanisms of recovery might be different following disturbances that encompass large areas (hundreds of metres to kilometres), and there is growing evidence that the role of seeds in recovery may be important when large areas of seagrass are lost. Understanding the mechanisms of recovery in those situations, and the potentially important role of seeds or advected vegetative fragments, would increase the ability to predict the rate of recovery and to evaluate the importance of neighbouring seagrass meadows for meadow recovery post-dredging. Gaining this understanding may require an opportunistic, but well-coordinated, approach that takes advantage of commercial dredging projects in the vicinity of known seagrass habitat, or the approval to implement large-scale experimental dredging. Modelling studies that incorporate seagrass growth patterns (with parameters relevant to the Pilbara) to predict the length of time required to recover from disturbances of different intensities and spatial extents would complement field experiments, and enable prediction of outcomes at spatial and temporal extents for which field experiments are not logistically feasible. Such models could be validated by comparisons against outcomes of field experiments.

1 Introduction

Seagrasses are highly valued for the range of ecosystem functions and services they provide (Short et al. 2007), including their importance as food sources to threatened species of animals (e.g. green turtles and sirenians). Disproportionately higher abundances of species are supported by seagrass habitat compared to other soft-bottom marine habitats, and many seagrass meadows support high rates of carbon sequestration (McLeod et al. 2011). Seagrasses face numerous pressures; globally more than a quarter of the area formerly covered by seagrass has disappeared and the rate of loss is accelerating (Waycott et al. 2009). However, within this broad trend, seagrass areal extent has increased at some locations (e.g. Macreadie et al. 2014), demonstrating that recovery from seagrass loss is possible when conditions are favourable.

In some places, loss and recovery of seagrass over relatively short periods of time (months to years) is a natural phenomenon, which is influenced by changes in environmental variables such as temperature, light and salinity — and in some cases might be as a result of consumption by herbivores (Eklof et al. 2008, Fourqurean et al. 2010). In these places, distinguishing losses that are caused by human activities (such as dredging-induced decreases in light or increases in sedimentation) from natural losses is challenging. Understanding where, when and how seagrasses recover from disturbances is important when assessing the likelihood of seagrasses to recover from disturbance, and predicting the length of time such recovery might take.

Recovery from disturbance relies on three major mechanisms:

- vegetative growth from remaining plant material within or immediately adjacent to the disturbed area;
- vegetative regrowth from fragments of plants that are advected into the area; and
- recovery from seeds, either in a sediment seedbank or that are advected into the area.

Despite this general understanding, there are few studies that unambiguously separate the relative importance of these mechanisms of recovery among seagrass species. Most relevant to this study are the small-leaved species of seagrass that typically occur in the north west of Western Australia (e.g. from the genera Halodule and Halophila) that have relatively low resistance to disturbance but frequently display the ability to recover rapidly (York et al. 2015). Experiments testing the mechanisms of recovery of these tropical seagrasses have revealed a complex and inconsistent story. In the tropical and sub-tropical USA, studies showed a high dependence on vegetative regrowth for recovery of seagrasses following disturbance, though this could vary among species within the meadows (Kenworthy et al. 2002, Rollon et al. 1999). In Queensland, experiments found that, up to two years following loss, seagrass recovery only occurred at deeper sites where *Halophila* spp. had the capacity to recover from seed banks (Rasheed 2004, Rasheed et al. 2014), while seagrass in shallower water had poor seed reserves, relied on vegetative growth for recovery, and had much slower recovery rates. Similarly, Rasheed (2004) found that *Halophila ovalis* (R.Brown) J.D.Hooker was able to colonise cleared plots from seeds within a few months, but also found that other species of seagrass became more dominant after longer periods. Notably, that study also found that Tropical Cyclone Justin substantially reduced the cover of *H. ovalis*, but not other species present. Taylor et al. (2013) found that subtidal *H. ovalis* and *Halophila spinulosa* (R.Brown) Ascherson were able to recolonise small cleared patches through vegetative regrowth, but not from seeds, within 4 to 6 months. Rasheed et al. (2014) emphasised the need to understand inter- and intra-specific differences in seagrass recovery when predicting the consequences of disturbance.

The objective of this project was to determine whether seagrasses in the north west of Western Australia can recover following disturbance, the length of time needed for recovery and the likely mechanism. Given the apparent variability in dependence on sexual and vegetative mechanisms of recovery (see above), our study attempted to distinguish between asexual recovery (via rhizome elongation from existing plants) and sexual recovery (from seeds) in seagrass meadows. To do this, we conducted a field experiment at Thevenard Island in the Pilbara region of Australia. All seagrass was removed from experimental plots within a seagrass meadow, and recovery mechanisms were evaluated by comparing plots in which lateral extension of rhizomes was prevented by a barrier (and therefore recovery was dependent on seeds or advection of vegetative fragments) with plots in which no barrier was present. The experiment was not intended to parameterize the rate of recovery following dredging disturbance (which is a focus of WAMSI DSN Project 5.5), although we did intend to provide context for interpretation of the laboratory experiment results in WAMSI DSN Project 5.5 (Statton et al. 2017a, Statton et al. 2017b, Statton et al. 2017c).

2 Materials and Methods

The experimental design focussed on using barriers to test questions about vegetative vs seed-mediated recovery. Initially, we planned to manipulate the presence of seeds as part of the experiment, but this was not possible. Within the WAMSI DSN Project 5.3 Natural Dynamics, we examined sediment cores to determine seed abundance and to test our ability to collect seed for use in the experiment. The examinations were made both visually and by a density separation method using Ludox® TM-40. The (wet) sediment was passed through 1 mm, 0.5 mm and 0.25 mm sieves. The 1 mm fraction was visually examined. The vast majority of cores did not contain any seeds, but a small proportion of cores contained *Halodule uninervis* (Forsskål) Ascherson seed coats and *H. ovalis* fruits. No seeds were found in the 0.5 mm and 0.25 mm fractions. To determine whether the density separation method would detect seeds if they were present, *H. ovalis* seeds were placed within sediment known to have no seeds. On average, 90% of the seeds were retrieved, giving us confidence that seeds would be found if present. We concluded that we had no ability to control the presence or absence of a seedbank, because the low densities made it impractical to obtain a sufficient amount of seed.

The experiment was conducted at two sites near Thevenard Island; one site was at a depth of 2 m and termed the 'Shallow' site (21.46212 S, 115.02539 E) and the other at a depth of 6 m and termed the 'Deep' site (21.47361 S, 115.00725 E). Both sites comprised homogeneous sandy sediments (relatively fine sands at the Deep site and coarser sand/rubble at the Shallow site) of consistent depth. At each site, two types of treatments were imposed: Clearing (cleared, uncleared) and Barriers (with barrier, without barrier) (Table 1). Twenty four circular plots (diameter 75 cm) were established. Twelve of these plots were completely cleared of all seagrass by hand. Six of the cleared plots were surrounded by a black propylene plastic border sunk into the sediment to a depth of 6 cm to prevent rhizome extension from the surrounding meadow, and the remaining six cleared plots were left without a border to allow rhizome extension. Of the 12 uncleared plots, 6 were surrounded by a plastic border into which gaps had been cut (allowing seagrass rhizomes to grow through), thereby creating a procedural control to verify whether the presence of the border itself influenced the ability of seagrass to grow within the plot. The remaining 6 uncleared plots were not manipulated in any way. The treatments, and the underlying questions which each addressed, are shown in Table 1.

Table 1: Experimental treatments employed, and the underlying question that each addresses.

	cleared	**uncleared**
with barrier	Treatment A Tests whether recovery occurs via seed or advected plant fragments	Treatment C Procedural control with partial barrier: tests for effect of barrier
without barrier	Treatment B Tests whether recovery occurs via vegetative regrowth from adjacent meadow	Treatment D Control, not manipulated in any way: tests whether the seagrass meadow changes naturally during the experiment

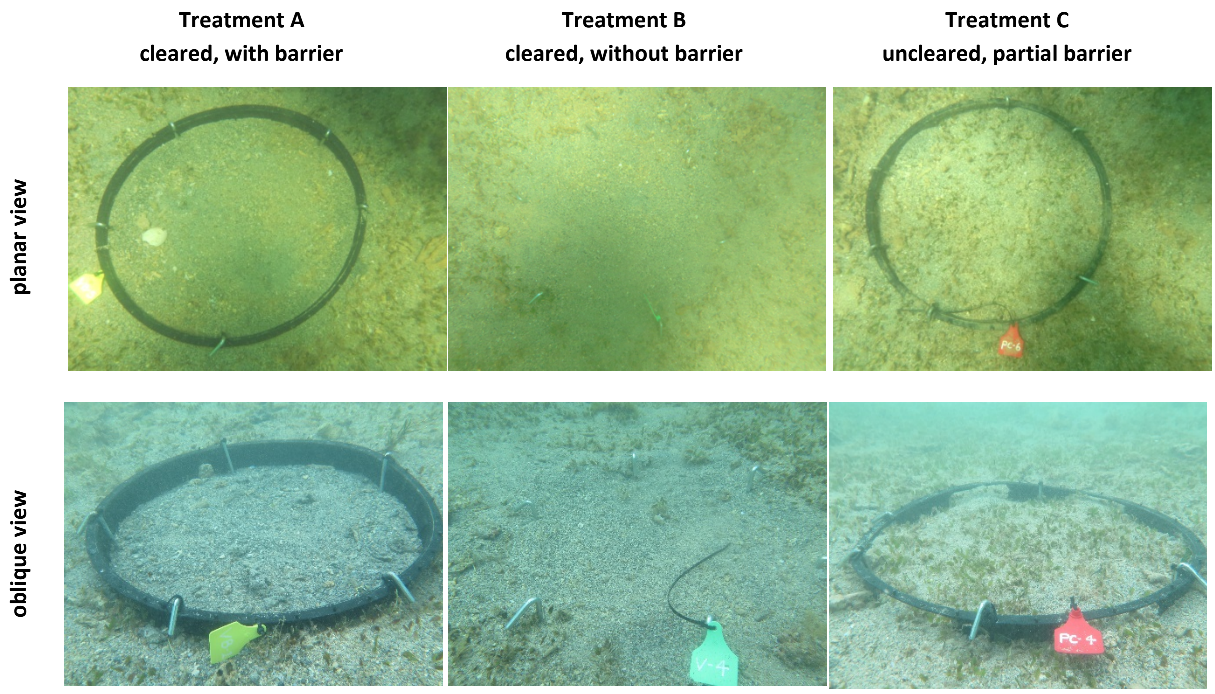

Figure 1. Photographs of example plots in the 3 manipulated treatments (Treatment A, Treatment B, Treatment C). The partial barrier in Treatment C appears whole from above, but was perforated below the rim (see bottom right panel), allowing rhizome growth into the plot.

The experiment was established on the 14 and 15 of November 2014, and the experimental plots monitored after 8, 21, 59 and 104 days. Final sampling was to be taken in June 2015, but in March 2015 Tropical Cyclone Olwyn (Category 3) passed within 40 km of Thevenard Island, and when the experiment was visited on 10 June 2015 (208 days after establishment), none of the experimental apparatus (borders, tags, star pickets) remained at the Shallow site. The plots were intact at the Deep site, but visibility was extremely poor, and although photographs were taken they could not be analysed with confidence. Biomass (see below) was measured in the experimental plots at the Deep site on the final date (11 June 2015).

On each date, photographs were taken of each plot. Divers also produced diagrams of any seagrass growth in cleared plots. Each photograph was analysed using TransectMeasure® software. A random array of 200 dots was placed over the image of the plot, and for each dot an operator (R. McCallum on all occasions) identified the substrate immediate underneath as seagrass (recording the species present), sediment, epibenthos or macroalgae. To further distinguish whether any regrowth was occurring from the edges of the plots (implying vegetative recovery) the dots were assigned into 'edge' (outer 20% of the plot) and 'centre' (inner 80% of the plot). The data were stored in an Oracle database and R (R Core Team 2014) software used to extract and analyse the data as percentage cover.

The data yielded by measurements of seagrass cover during the experiment were analysed by repeated-measures ANOVA, with the primary hypothesis that that recovery through vegetative growth from outside the plots would be evident as differences in edges versus centres of plots from different treatments, and that these differences would vary at each date (as seagrass cover increased). We were therefore most interested in the test of the interaction between Treatment × Date × Position (where Position refers to the edge or centre of a plot).

3 Results

3.1 Shallow site

At the Shallow site, there was a statistically significant Treatment × Date × Position interaction in total seagrass cover (MS = 166.4, F = 3.7, P< 0.001). Images of plots that represent the patterns observed are shown in Figure 2. As expected for a 3-way interaction, the nature of differences was complex, but three patterns emerged:

- cleared plots with no barriers (Treatment B) were not significantly different to cleared plots with barriers (Treatment A) on the first three dates surveyed, but by February 2015 (59 days) they were different, with more cover in the plots with no barrier;
- cleared plots with no barriers (Treatment B) were significantly different (less cover) to control plots (Treatment D) during the first three dates surveyed, but were not different to control plots by February 2015 – 59 days after the experiment was established (this pattern was present at both the edges and centres of plots);
- cleared plots with barriers (Treatment A) were significantly different (less cover) to uncleared control plots (Treatment D) throughout the experiment; and
- control plots (Treatment B) typically did not show significant differences to uncleared procedural control plots (Treatment C) throughout the experiment.

These results reflect that there was recovery of seagrass in cleared plots without barriers, but no recovery in cleared plots with barriers (Figures 2, 3 and 4). During the course of the experiment, there was a decline in seagrass cover in uncleared plots with and without barriers (Treatments C and D).

Additional evidence for regrowth from the edges of cleared plots would be a difference in the relative cover of seagrass at the edges versus the centres of plots during the initial phase of colonisation, a pattern that should weaken and then disappear as colonisation progresses. At the Shallow site, there was a statistically-significant difference between the edges and centres of plots; this difference was present at the beginning and end of the experiment (χ^2 >10, P <0.001), but not in January 2015 (χ^2 = 3.8, P = 0.05). Patterns in the location of seagrass on each date confirm the interpretation that recovery occurred via regrowth from the edges of plots (Figure 5).

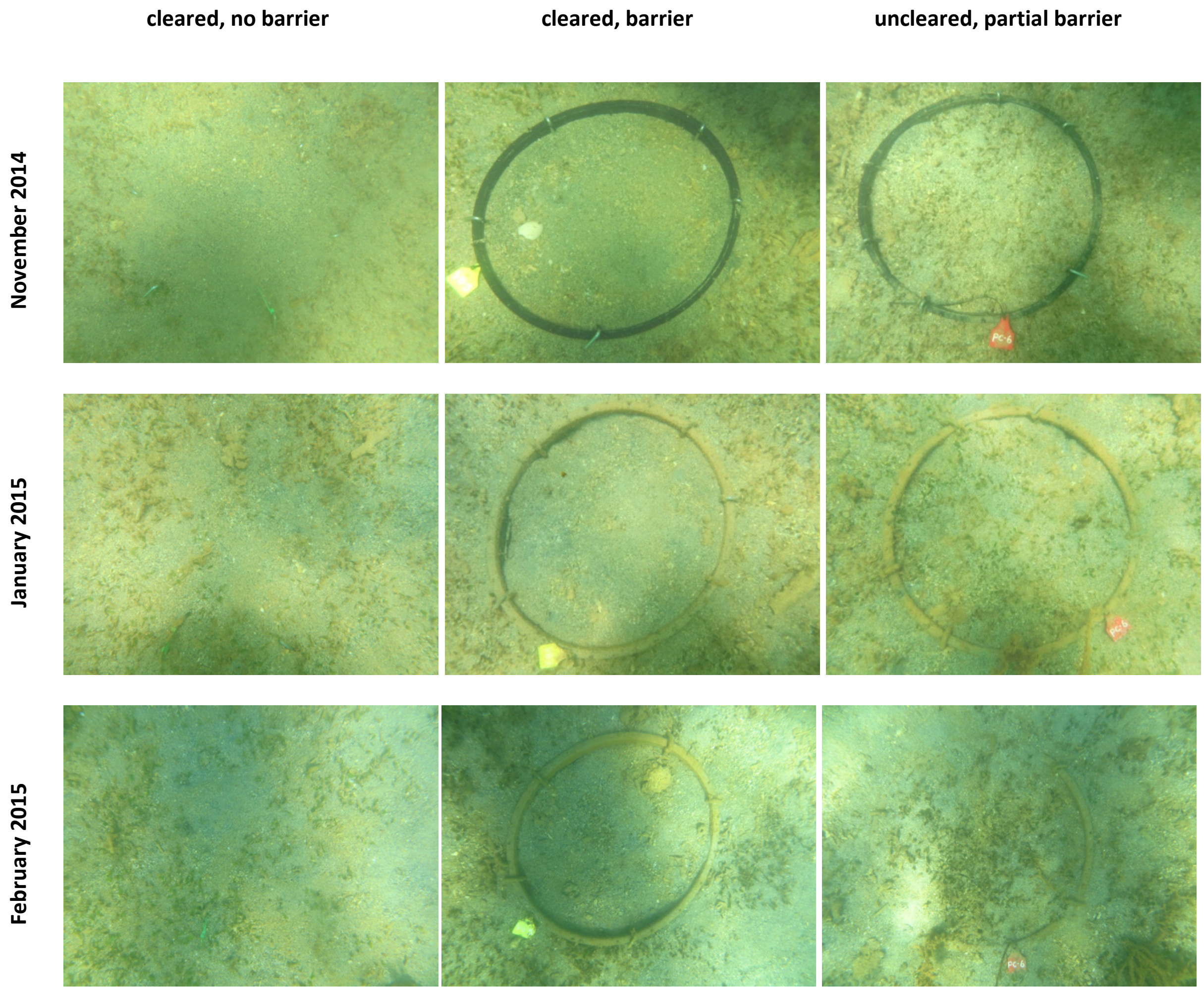

Figure 2. Photographs of seagrass in example plots of the 3 manipulated treatments during November 2014, January 2015 and February 2015. These times encompass the first three months of the experiment and illustrate the different patterns of recovery in the different treatments. Cleared plots with no barrier (Treatment B) show recovery, commencing at the edges, while cleared plots with a barrier around them (Treatment A) show no recovery. The procedural control (uncleared but with a partial border, Treatment C) shows no noticeable change.

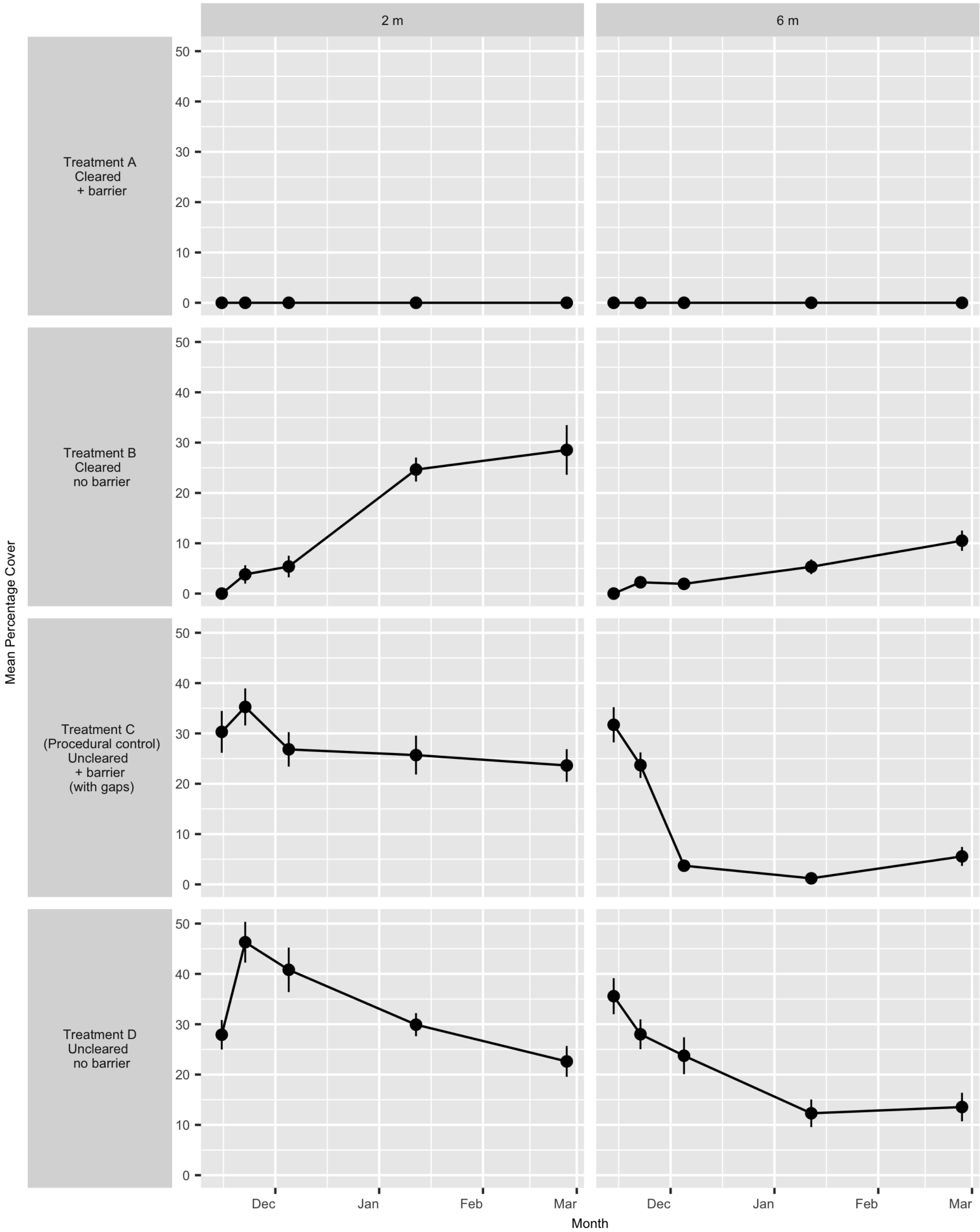

Figure 3. Patterns in total seagrass cover within cleared and uncleared seagrass plots at (left column) the Shallow site (depth 2 m) and (right column) the Deep site (depth 6 m). All data are means ± SE, n=6. At both sites, the cleared plots with surrounding borders (top row) showed no increase in cover over time, while the cleared plots with no borders (second row) showed increases in cover, eventually recovering to levels comparable to the uncleared control plots (bottom row).

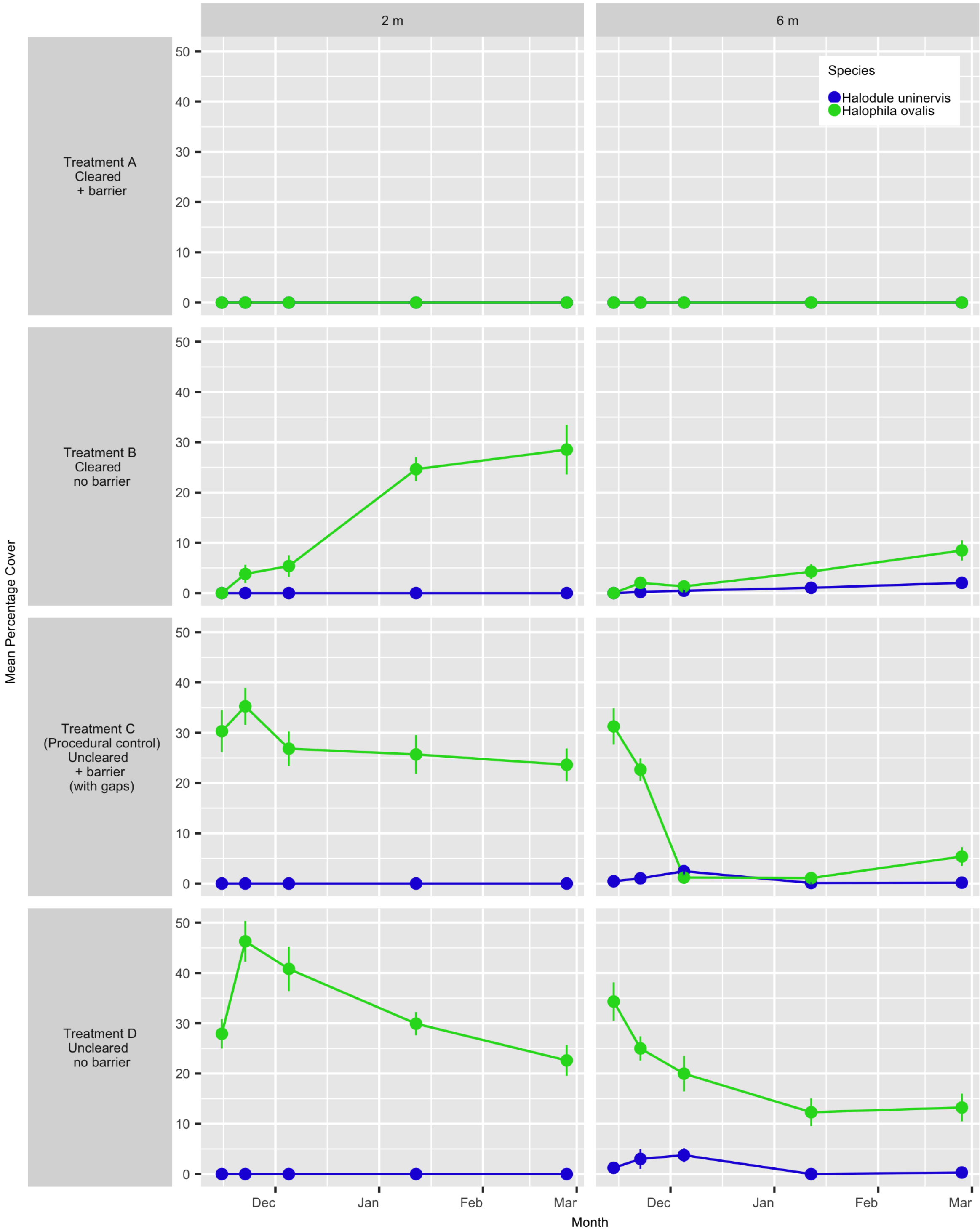

Figure 4. Patterns in cover of *Halophila ovalis* and *Halodule uninervis* within cleared and uncleared seagrass plots at the (left column) Shallow site and (right column) Deep site. All data are means ± SE, n=6. Overall, most of the change in seagrass cover in cleared plots was due to an increase in the cover of *H. ovalis*.

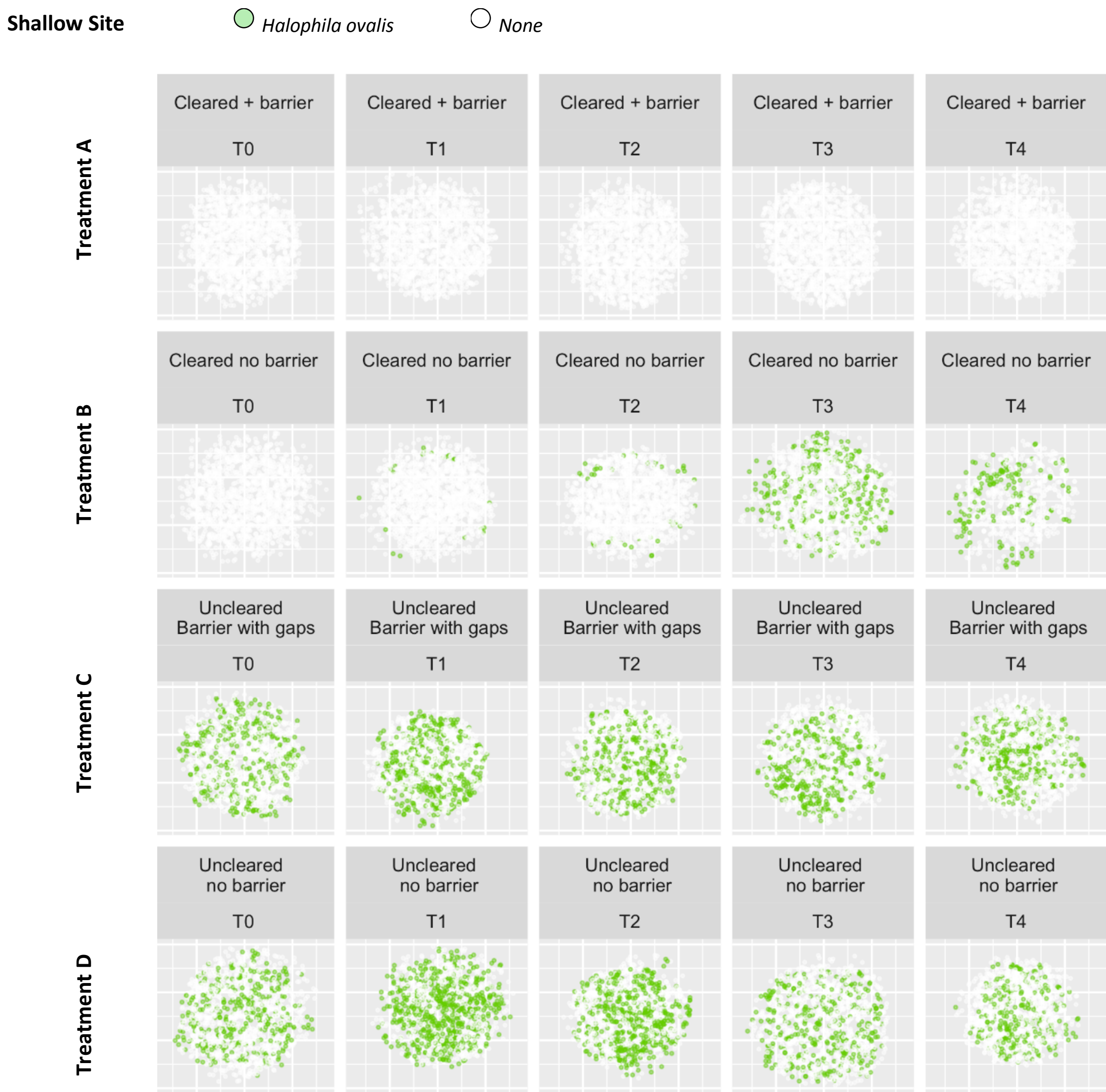

Figure 5. Shallow site seagrass recovery. Plots of *Halophila ovalis* presence in each of the cleared and uncleared seagrass plots at the Shallow site (depth 2 m) over time. Green dots indicate the presence of a seagrass shoot, pooled across all six replicate plots. White dots indicate no seagrass was present. T0 = 24 Nov 2014 and T1 = 8 d, T2 = 21 d, T3 = 59 and T4 = 104 d later. The diagrams demonstrate that in cleared plots where seagrass cover increased (Treatment B) the recovery commenced at the edges of plots, consistent with recovery through rhizome extension from the surrounding meadow.

3.2 Deep site

At the Deep site, there was no statistically-significant Treatment × Date × Position interaction in total seagrass cover (MS = 26.0, F = 0.9, P = 0.5). However, there was a statistically-significant Treatment × Date interaction (MS = 797.9, F = 29.3, P <0.001). From analyses of pairwise comparisons of this interaction, the following patterns emerged:

- cleared plots without barriers (Treatment B) were not significantly different to cleared plots with barriers (Treatment A) during the first three dates surveyed, but by February 2015 (59 days) they contained significantly higher cover;

- cover in cleared plots with barriers (Treatment A) was significantly lower than uncleared plots without barriers (Treatment D) on all dates;
- cleared plots without barriers (Treatment B) were significantly different (containing lower cover) to uncleared plots without barriers (Treatment D) on the first three survey dates, but not during January or February 2015; and
- uncleared plots without barriers (Treatment D) yielded statistically-significant differences to uncleared plots with barriers (Treatment C) in January and February 2015.

These results reflect that although there was recovery of seagrass in cleared plots without barriers, and no recovery in cleared plots with barriers, there was a substantial decline in seagrass cover in uncleared plots (Figures 3, 4 and 6). The decline in cover in the uncleared plots with barriers was more extreme, so that it had significantly lower cover than uncleared plots without barriers by the end of the experiment. This pattern confounds interpretations about rates and magnitudes of recovery; however, the recovery of seagrass in the cleared plots without barriers, but not in the cleared plots with barriers, is consistent with the result found at the shallow site. This recovery also occurred despite a trend for decreasing cover in the uncleared plots.

There was a statistically-significant difference between the edges and centres of cleared plots without barriers in November and December ($\chi^2 > 20$, $P < 0.001$), but not in January or February ($\chi^2 = <1$, $P > 0.5$). Patterns in the location of seagrass on each date confirm the interpretation that recovery occurred via regrowth from the edges of plots (Figure 6).

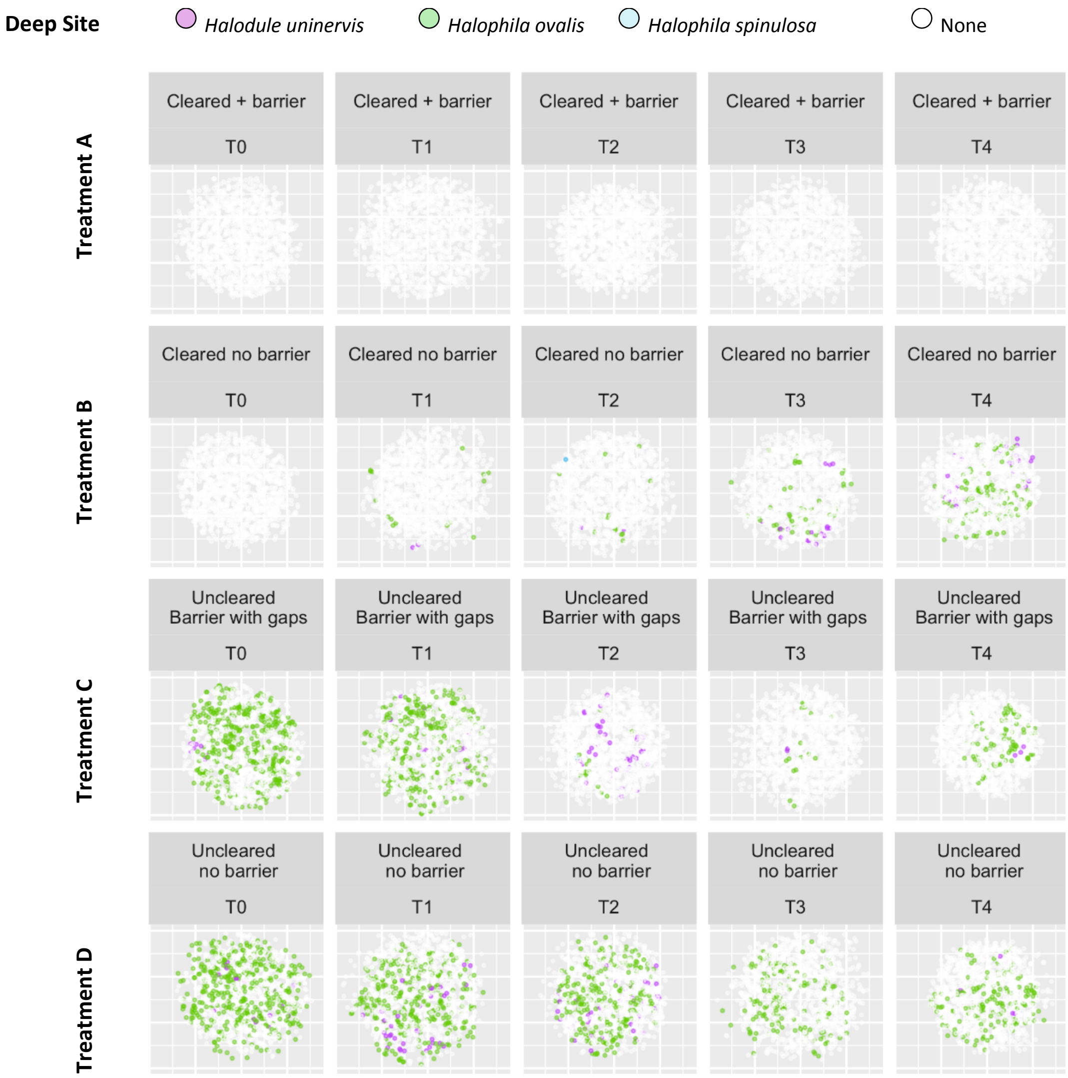

Figure 6. Deep site seagrass recovery. Plots of seagrass presence in each of the cleared and uncleared seagrass plots at Shallow site (depth 2 m) over time. Green dots indicate the presence of a seagrass shoot, pooled across all six replicate plots. White dots indicate no seagrass was present. T0 = 24 Nov 2014 and T1 = 8 d, T2 = 21 d, T3 = 59 and T4 = 104 d later. The diagrams demonstrate that in cleared plots where seagrass cover increased (Treatment B) the recovery commenced at the edges of plots, consistent with recovery through rhizome extension from the surrounding meadow.

4 Discussion and Conclusions

The objective of this project was to determine the capacity of seagrasses to recover from disturbance as well as the timeframes and mechanisms of recovery, including the relative importance of sexual or asexual recovery. Despite the premature end to the experiment due to Tropical Cyclone Olwyn, our results show that the primary mechanism for recovery of seagrass (comprising mostly *H. ovalis*) at Thevenard Island was through vegetative regrowth, and that the length of time it took 75 cm diameter (~0.5 m^2) cleared patches to fully recover was 2 to 3 months. The patterns of seagrass recovery in the experimental clearances showed unambiguously that recovery occurred through vegetative regrowth from the edges of cleared patches. There was no recovery of seagrass from the centres of plots or in plots with barriers, so there was no evidence of recovery from seeds or from fragments of plants that might have drifted into the plots. This finding is consistent with the near-complete absence of seeds in the cores that were examined in the companion project on seagrass natural dynamics (WAMSI DSN Project 5.3; Vanderklift et al. 2017). It is also consistent with the findings from shallow-water (<6 m) seagrass meadows in Queensland, which had very slow recovery following disturbance, attributed to the limited presence of seeds and reliance on vegetative growth for recovery (Rasheed et al. 2014). The experiment was initiated in November 2014, the period of flowering and seed production (see WAMSI DSN Project 5.3).

At the Shallow site, regrowth of seagrass led to cover in the cleared plots without barriers that was indistinguishable from control plots after two months. In contrast, no seagrass was recorded in any cleared plot with a barrier. At the Deep site, the patterns were qualitatively similar, but interpretations are somewhat confounded by loss of seagrass cover in the uncleared plots, and an apparent effect of the barrier. Nevertheless, consistent with patterns observed at the Shallow site, there was regrowth of seagrass in cleared plots without barriers, but no seagrass was recorded in any cleared plot with a barrier.

There was a complete loss of seagrass at the Shallow site, and a precipitous decline in seagrass at the Deep site by June 2015, which was likely caused by Tropical Cyclone Olwyn. The likely mechanism of these losses is physical disturbance by waves (at the Shallow site all the plot barriers and marker pegs were missing), although there was also a period of very low light immediately following Tropical Cyclone Olwyn, which may have placed any surviving plants under light-limitation, preventing their re-growth.

Our ability to generate broad inferences about the ability of seagrass in the Pilbara to recover from disturbance relies on several assumptions. The following are likely to be the most critical assumptions:

- the seagrass and environmental conditions present in the study area is representative of seagrass in the Pilbara;
- recovery from patches ~0.5 m^2 is representative of recovery from larger patches; and
- the experimental clearances were representative of the nature of disturbance expected from dredging.

4.1 Representativeness of seagrass and study site

At Thevenard Island, *H. ovalis* was the most abundant species — it was the only species observed at the Shallow site, and it was far more abundant than *H. uninervis* at the Deep site. *H. ovalis* is the most abundant species throughout the Pilbara (and is also widespread throughout the north west of Western Australia: see McMahon et al. 2017b), although there is considerable variation in the species of seagrass present at different places; six species were recorded in the companion study of spatial and temporal variation, of which only *H. ovalis* was present at all locations and sites surveyed (see WAMSI DSN Project 5.3 Natural Dynamics). The cover of seagrass (average 33% at the Shallow site and 22% at the Deep site) was within the range recorded at other sites, and the temporal variation recorded at both Thevenard Island sites was also within the range of temporal variation recorded at other sites in the Pilbara (see WAMSI DSN Project 5.3 Natural Dynamics). Photosynthetic photon flux density (PPFD-benthic light) measured at the study site was within the range of PPFD measured at other locations and sites surveyed (see report for WAMSI DSN Project 5.3 Natural Dynamics). All variables measured at the study site were, therefore, within the range recorded at other places in the Pilbara. Nevertheless, the extensive variation in the abundance and species composition of seagrass throughout the Pilbara means that findings at one location might not be readily transferred to all other locations.

Some sense of the general mechanisms and ability of tropical seagrass to recover from disturbance can be generated by comparison of our study with similar studies elsewhere. Rasheed et al. (2014), found that a shallow (2 m depth) meadow dominated by *H. uninervis* was not able to recover from seeds within two months, though meadows at 14 m depth, dominated by *Halophila spinulosa* and *Halophila decipiens* (Ostenfeld) were able to recover from seeds. Similarly, Rasheed (2004) found that *H. ovalis* was able to colonise cleared plots from seeds within a few months at a location with a mean depth of 3.8 m, but also found that other species of seagrass became more dominant over a longer duration. Notably, that study also found that Tropical Cyclone Justin substantially reduced the cover of *H. ovalis*, but not other species present. Taylor et al. (2013) found that subtidal *H. ovalis* and *H. spinulosa* were able to recolonise small cleared patches through vegetative regrowth, but not from seeds, within four to six months. Similarly, York et al. (2015) noted that a deep-water seagrass meadow did not re-establish in the year following dredging, but did in the subsequent year. Overall, then, there is emerging evidence that while sexual reproduction may be important for the re-establishment of seagrass meadows, its role may be most critical when the meadow is completely lost and there is no possibility of rapid re-establishment from vegetative growth.

While robust generalisations cannot be made from this limited set of experiments, we note that in the above studies it was the shallowest (2 m depth) sites that failed to recover from seed. It is plausible that depth may affect the presence and viability of seed banks. Low hydrodynamic forcing at depth may favour the persistence of a seed bank. It is therefore possible that recovery from seeds might occur elsewhere in the Pilbara region, though we note that few viable seeds were found in the sediment at any site surveyed in the Pilbara during the natural dynamics survey (WAMSI DSN Project 5.3).

4.2 Representativeness of clearance size

The spatial extent of seagrass loss following dredging events can encompass hundreds of hectares or more (see Erftemeijer & Lewis 2006, York et al. 2015). Our experimental clearances, like those of others, are several orders of magnitude smaller than this. It is likely that mechanisms that result in recovery of meadows depend on the spatial extent of the impact. Across relatively short distances (e.g. metres or less) vegetative recovery might be an efficient mechanism for colonising space. Such a mechanism would be effective at colonising gaps created within meadows. While large dredging projects would be expected to affect light availability and sediment deposition on much large spatial scales than simulated in our study, other dredging-related activities (e.g. anchoring) will typically cause disturbance on the scale of our experimental treatments and at that scale we could expect relatively rapid recovery (weeks to months), assuming the adjacent meadow is available as a source for recolonisation.

Recovery over greater spatial extents can occur through vegetative growth but this typically takes longer (Walker et al. 2006). Rates of patch growth are non-linear, strongly affected by several plant-specific growth characteristics and typically increase with the size of the patch (Sintes et al. 2006). This makes a simple extrapolation of our results to larger areas inappropriate. However, even the highest modelled growth rates suggests meadow extension rates in the order of 0.1 to 1.0 m y^{-1}, indicating that this is unlikely to be an effective mechanism for rapid recovery of disturbances at the scale of 100 to1000 m^2, at least in the absence of significant immigration of vegetative fragments. The relative rapidity of recovery of seagrass following episodes of absence or very low cover across large extents in the study region (e.g. Loneragan et al. 2013, see also Vanderklift et al. 2017) suggests that some recruitment from seeds is very likely. Nevertheless, we did not record any such recruitment, and our surveys showed low abundances of viable seeds across the study area.

4.3 Representativeness of nature of disturbance

Our experiment tested the effect of complete removal of seagrass. Seagrass abundance can be negatively impacted by decreased light, altered light quality and increased sediment deposition (McMahon et al. 2017b), as well as direct physical disturbance. In severe cases, these impacts can lead to complete loss of rhizomes and roots as well as leaves following dredging (Erftemeijer & Lewis 2006). Our experimental clearance was, therefore, representative of the most severe of the impacts expected from dredging — albeit at a limited spatial extent.

4.4 Conclusion

Despite the inability to run the experiment for the intended six-month duration due to the impact of Tropical Cyclone Olwyn, the results indicated unambiguous evidence of recovery from vegetative regrowth at both sites, and no evidence of recruitment from seeds. Recovery was rapid, occurring within two months, and was primarily due to recolonisation of cleared plots by *H. ovalis*, indicating that recovery from disturbances causing small cleared patches could take weeks to months. On the other hand, if dredging were to result in large-scale loss of meadow, then recovery would rely on immigration of plant fragments or seed from distant sites, and will likely be much slower.

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