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Strategy for assessing impacts in ephemeral tropical seagrasses

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Abstract

We investigated the phenology and spatial patterns in *Halophila decipiens* by assessing biomass, reproduction and seed density in ~400 grab samples collected across nine sites (8 to 14 m water depth) between June 2011 and December 2012. Phenology correlated with light climate which is governed by the summer monsoon (wet period). During the wet period, sedimentary seed banks prevailed, varying spatially at both broad and fine scales, presenting a source of propagules for re-colonisation following the unfavourable growing conditions of the monsoon. Spatial patterns in *H. decipiens* biomass following monsoon conditions were highly variable within a landscape that largely comprised of potential seagrass habitat. Management strategies for *H. decipiens* and similar transient species must recognise the high temporal and spatial variability of these populations and be underpinned by a framework that emphasises vulnerability assessments of different life stages instead of relying solely on thresholds for standing stock at fixed reference sites. .

Keywords: disturbance; *Halophila decipiens*; life-history; management; phenology; resilience

Introduction

Assessing the impact of anthropogenic development and construction on plant communities often focuses on the adults in a population, overlooking other life history stages like mobile seeds, dormant seeds in seed banks, and recruiting seedlings (Damschen et al., 2008). This is especially the case for seagrasses where the focus for impact assessment has been the standing stock of adults (Marbà et al., 2013). This seems appropriate as seagrasses have extensive clonal spread through vegetative growth. Yet, they also have active sexual reproduction that varies over spatial scales of meters to kilometres and in timing from weeks to months with strong interannual variation (e.g. Campey et al., 2000; Fonseca et al., 2008). These reproductive events produce seeds that can be transported 100s of kilometres (Kendrick et al., 2012b; Ruiz-Montoya et al., 2012, 2015) or form seed banks in mobile coastal sediments (Fonseca et al., 2008).

Seagrass monitoring programs have traditionally focussed on biomass, % cover or shoot density as indicators of stress (Marba et al., 2013). For example, the majority of monitoring programs in European seagrass meadows examine changes in the vegetative abundance of seagrasses, as shoot density or cover (Marbà et al., 2013). However, these indicators have been developed to assess loss to perennial seagrass species (e.g. *Posidonia* spp., *Thalassia* spp., *Zostera* spp.) that persist as continuous meadows. In the tropics, *Halophila spp.* are common and can cover vast areas of the deep subtidal (Lee Long et al., 1993, Fonseca et al., 2008.). The species *Halophila decipiens* occurs in deeper, light-limited environments, is small and has low % cover and shoot density naturally, is an annual in many regions, or highly seasonal as meadows, and is highly fecund, producing seeds that can remain dormant in sediments through periods of low light availability and poor growing conditions (McMillan, 1989; Kenworthy, 2001;Rasheed et al 2014; York et al 2015). The timing of seed release from fruits, quantities of seeds in sediments and conditions required for seed germination are influenced by local environmental conditions, particularly light availability

(Kenworthy, 2001). The resilience of *H. decipiens* is therefore in the persistence of a seed bank, and rapid germination growth and reproduction when environmental conditions are favourable. Monitoring programs that rely solely on characterizing changes in shoot density, cover or biomass in perennial meadows may not be appropriate for this species.

Our study location, James Price Point was proposed as a port in the Kimberley Region of northern Australia. The Kimberley Region has a coastline of approximately 13,000 km that includes extensive island archipelagos and marine embayments. Tides in the Kimberley are among the largest observed in tropical regions globally (12 m maximum) although over much of the region spring tides are <6 metres. The climate is dry tropical with a distinct monsoonal season (October to April). Globally, tropical seagrasses provide ecological functions and services in coastal and nearshore areas, including being the foundation to the trophic system, are critical habitats to rare and endangered mega fauna such as dugongs and turtles, that are of significant indigenous cultural and economic value (Unsworth and Cullen 2010). In the Kimberley Region, there has been few studies of the structure and function of intertidal and subtidal seagrasses (Walker and Prince, 1987), so it is difficult to develop meaningful environmental thresholds that are relevant to the region (Erftemeijer and Lewis, 2006). Recently, there has been rapid expansion of development in the Kimberley that may threaten coastal ecosystems, driven by the offshore oil and gas industry, port expansion to support oil and gas and mining, new tourism activities, and aquaculture (Wood and Mills, 2008). As such, there is a need for research that informs regulators of the critical life history phases and transitions for seasonally abundant seagrass species.

We describe an approach to assessing seagrass loss and for monitoring both resistance and recovery of naturally ephemeral seagrass beds using the species *Halophila decipiens*. We describe the phenology of growth, reproduction, seed release and seed germination of *H. decipiens* at James Price Point over 18 months. We further relate the life history transitions to changes to environmental variables, including water temperature, salinity, chl a in the water column, turbidity and % light reaching the benthos. We then summarize potential environmental drivers and life history transitions in *H. decipiens* into a temporal assessment of critical times in a year that will require managing impacts of dredging and port development.

Methods

The study location was 50 km north of Broome, Western Australia (17° 28' 51 S, 122° 07' 06 E) near James Price Point and covered an 60 km^2 (9 m to 14 m deep) (Figure 1). Benthic sampling was restricted to remote methods. Sediment samples were collected across nine sites using a Petite PONAR® sediment grab (152mm x 152 mm) over nine sampling events between July 2011 and December 2012 to assess seed density and seagrass cover. A remotely operated vehicle (ROV) fitted with a camera was also used to assess seagrass cover over seven sampling events between July 2011 and December 2012. High turbidity and poor weather conditions during the summer months (wet monsoon period) restricted the use of the ROV because of poor visibility resulting in less sampling events. . All sediment samples were kept cool by storing them on ice in the field and processing them immediately on return to the laboratory.

Seagrasses in video imagery were identified and percent cover estimated. Seagrasses in grab samples were identified and the number of flowers and fruits were recorded. Number of shoots (or leaf pairs for *Halophila spp*.) was not recorded as many of the seagrass in the grab samples were not intact making it very difficult to accurately count shoots. Seagrass was air dried and total biomass recorded.

Seed densities were calculated based on the method developed Hammerstrom and Kenworthy (2003b). Firstly, the volume of sediment for each sample was recorded. Sediment samples were then wet sieved in order to separate the sediment fraction ranging between 0.2 to 1 mm. *Halophila* seeds are generally between 0.4-0.8 mm in diameter (Hammerstrom and Kenworthy, 2003a). Seeds were then removed from the fractionated sediment using a density separation technique (Hammerstrom and Kenworthy, 2003b). On average, this sieved portion of sediment could be separated into at least five replicate sub-samples of 2 cm^3 which were placed in centrifuge tubes. For each sub-sample, 10 ml of chilled Ludox (sigma-aldrich colloidal silica 40%) was added to each tube as the extract solution. Tubes were capped, shaken vigorously for 20 seconds and then centrifuged at 2500 rpm for 10 minutes. Most inorganic sediment particles settled to the bottom off the ludox, while organic matter (including seeds) floated at the top of the tube. This supernant was then removed from the tube using a pipette, and transferred to a Petri dish and seeds counted under a dissecting microscope (40 x magnification).

The mean number of seeds per replicate was converted to the mean number of seeds per m^2. We based our calculation on the McMillan and Soong (1989) method, where 300 cm^3 of sediment volume was the equivalent to 100 cm^2, or 0.01 m^2. The major assumption of this method is that seeds are uniformly distributed in the sediment, which almost certainly does not hold true (Inglis, 2000). However, in the absence of controlling sample area in the field, this technique provides a good, albeit conservative, representation of the number of the seeds in a unit area of sediment, allowing comparisons between sites and over time.

Water quality was monitored at depth between December 2010 and November 2012 at six of the nine sites. Frames containing a Seabird SBE16+ with a SEACAT and an ECO-PAR were deployed at ~0.5m above the bed. The instruments measured and logged temperature, salinity, pressure, turbidity, chlorophyll and photosynthetically active radiation (PAR) at 30 minute intervals. A LiCor terrestrial PAR sensor was also used on land to capture PAR terrestrial readings at James Price Point Meteorological station. The data was then cleaned to include only valid readings, leaving only diurnal measurements for light readings. The data was averaged to monthly values in order to capture temporal changes. Sediment traps constructed to conform to the design specifications of Storlazzi et al. (2011) were deployed at all water quality monitoring sites, with deployment periods of approximately 6 to 8 weeks. Dry weights of sediment were assessed from traps.

We used Mann-Whitney U tests to examine differences in seed densities between sampling times. We used Kruskal-Wallis tests to examine the relationship between seed density and seagrass standing stock, depth, and site location. The physical data recorded over two years across six of the sites were grouped according to either wet or dry periods. A one tailed t-test at 99% significance was performed to test for differences between wet and dry periods. All analyses were performed using R version 3.2.2 (R Core Team 2015).

Results

Halophila decipiens was the only seagrass species collected in grab samples or seen in the ROV imagery. Rhizomes, leaves and roots were observed in grab samples collected between April and December, with biomass peaking towards the end of the dry period (October and November) (Figure 2A). This was reflected in the ROV imagery, with seagrass cover generally peaking across all sites in October/November over consecutive years (Figure 3). There was no seagrass (rhizome, leaf or root material) present in grab samples during the wet period (January) sampling period. Flowers were observed from July to November during the dry period, and fruits towards the end of the dry period, in October and November. Numbers of fruits per sample were highly variable at both fine (within site) and broad (between sites) spatial scales (Figure 2B), and were positively correlated to the amount of adult biomass present (Pearsons correlation coefficient = 0.67). There was an overall average of 45.4 ± 3.6 (s.e., n = 45) fruits per sample (range 0 to 96 fruits) and 29 ± 0.6 (mean ± se) seeds per fruit (range 12 to 46). Seeds were small and their size ranged from 0.35 to 0.58 mm in diameter (mean was 0.46 ± 0.003).

Seeds were found in sediments at most sample times, however, they were in higher densities from October through to January, following reproduction (Figure 2C, Mann-Whitney $P<0.0001/2.2 \times 10^{-16}$). Seed densities were greatest in November 2011, with a mean of 2800 ± 377 seeds m^{-2} across all sites and a maximum of nearly 14,000 seeds m^{-2} recorded at one of the southern-most sites (Figure 2D). There appears to be inter-annual variability of seed density in sediments, with greater seed numbers in October 2011 than October 2012 (Figure 2C, Mann Whitney $P<0.0001/3.3 \times 10^{-6}$). Similarly, greater seagrass biomass was recorded in October 2011 than October 2012 (Figure 2A Mann Whitney $P<0.0001/7.9 \times 10^{-7}$), which was also reflected in seagrass cover estimated from the ROV (Figure 3). Germinating seeds were first observed in April (approximately 15 m^{-2}), over the transition from wet to dry period, and continued to be found in lower densities throughout the growing period from June (approximately 5 m^{-2}) to August (approximately 4 m^{-2}). Emergent seedlings were only found in April (approximately 84 m^{-2}) and June (approximately 10 m^{-2}).

Seagrass biomass and seeds had high spatial variability at both broad (between site: kilometres) and fine (within site: metres) scales. There were no observed differences with depth (Kruskal-Wallis, $P = 0.23$) or distance from shore, or along shore (North to South Kruskal-Wallis, $P = 0.27$). However the spatial distribution in seed densities reflected the distribution of adult biomass (Figure 2C and 2D, Kruskal-Wallis, $P < 0.0001/3.6 \times 10^{-13}$)even over consecutive years.

Temporal and spatial patterns in physical environment

Water temperatures varied seasonally with minimum temperatures of ~21°C during the dry period (May to September), and significantly higher temperatures during the wet period ($P = 2.4\text{x}10^{-41}$), reaching temperatures of up to 33°C (January). Salinity on the other hand did not vary significantly and stayed at ~34 to 35 psu. Chlorophyll concentrations were significantly higher during the wet period ($P = 4.8\text{x}10^{-7}$, Figure 4), providing a proxy for increased nutrient availability into the system. Overall, irradiance reaching the water surface was significantly lower during the dry period ($P = 1.6\text{x}10^{-5}$, at ~ 860 µmol photons $m^{-2}s^{-1}$) than the wet period (~ 915 µmol photons $m^{-2}s^{-1}$). However, the turbidity levels (NTUs) were significantly higher during the wet period ($P = 4.1\text{x}10^{-6}$), reaching maximum averaged values of 36 NTU; with lower values (<5 NTU) and less variability during the dry period (Figure 4). As a result, more light reaches the seafloor during the dry period compared to the wet monsoon period and the amount of light depended on water depth. Sites in depths of 10 m or less (N2, M2 and S2) had up to 10% more irradiance on the bottom than those in 13-16 m of water (Figure 4), with these deeper sites receiving less than 5% surface irradiance (less than 45 µmol photons $m^{-2}s^{-1}$) during the wet period. Sedimentation rates were significantly higher during the wet period ($P = 0.0036$).

Discussion

Halophila decipiens appears to have a life history that is well suited to the dynamic Kimberley region in NW Australia (Figure 5). Despite total loss of adult biomass during the wet period (Figure 2A), the presence of a sedimentary seed bank allowed recolonization during the dry period, when environmental conditions were more conducive to seagrass growth. Similar patterns of occurrence have been shown for *H. decipiens* populations in NE Australia (York et al. 2015), suggesting that the seed bank is integral to the demographic resilience of this species to seasonal disturbance regimes (Kilminster et al. 2015). While the ephemeral nature of *H. decipiens* maintains a spatially and temporally heterogeneous subtidal landscape, which is dominated by phases of meadow loss and recovery, it presents difficulties for management. For instance, it is not possible to predict the specific location or size of *H. decipiens* meadows among sampling times, but the presence of meadows across our 60 km^2 sampling area was guaranteed during the favourable growing conditions of the dry period.

The temporal pattern in adult biomass of *H. decipiens* has recently been shown to be cued to annual changes in the benthic light climate (York et al. 2015). Similarly, we found that loss of adult biomass occurred with the onset of the wet period which was characterised by increased turbidity and decreased light availability at the seafloor (Figure 4). However, other forces associated with the onset of the wet in the Kimberley Region, like increased wave action leading to altered sediment dynamics, may also be contributing to seagrass loss. The ROV images provided anecdotal evidence of erosional and depositional events which can physically remove or bury adult biomass (Supplementary material, Figure 1). *Halophila decipiens* is adapted to survive such events via prolific seed production and the development of a sedimentary seed bank (Kenworthy, 2001). We did not observe seeds in the sediment over the entire year which suggests the seed bank of *H. decipiens* may be seasonal or transient, with high rates of seeds germination after the wet period (April) being the most likely contributing pathway to the re-establishment of seagrass beds in the region. Seeds of *Halophila spp.* have been shown to maintain dormancy for up to 24 months under laboratory conditions (McMillan, 1991). However, in natural settings, factors such as burial and predation contribute to seed mortality, and prevent the ability for a significant number of seeds to remain viable for longer than one year (Orth et al 1994, Orth et al 2007). Dispersal of these negatively buoyant seeds generally only occurs over metres to 10s of metres (Ruiz-Montoya et al 2012), with long distance dispersal (100's m to km's) possible during very energetic wave events (Bell et al 2008). This understanding of the seed characteristics implies some level of successful sexual reproduction is necessary each year to ensure the persistence of seagrass in the area. On the whole, the functional resilience of such transitory communities is highly dependent on sexual reproduction (Kilminster et al. 2015), and more understanding is needed on the movement ecology of seagrass seeds (McMahon et al. 2014).

The patterns we describe are not unique to this region of tropical Australia. York et al. (2015) recently demonstrated strong annual patterns in *H. decipiens* adult biomass at sites of similar depths on the NE coast of Australia. Fonseca et al. (2008) demonstrated the movement of *H. decipiens* meadows and the existence of a seed bank in unvegetated sediments in a 50 km region off the coast of Florida. This directly contrasts to seagrass species that have a life history strategy of persistence through clonal growth (both seasonally and inter-annually),where space is continuously occupied; resulting in large, continuous seagrass landscapes that persist over 10s to 1000s of km^2 and for 10s to 1,000s of years e.g. Owen Anchorage (Kendrick et al., 2000; Kendrick et al., 2008), Shark Bay (Kendrick et al., 2012a; Walker et al., 1988), Mediterranean (Arnaud-Haond et al., 2012; Kendrick et al., 2005). Given that seagrasses vary in their spatial and temporal persistence by orders of magnitude (Carruthers et al. 2007), a one-size-fits-all management approaches will not be suitable for all species and should be based around their specific life history strategy.

The practice of designating environmental windows for coastal developments and dredging that do not impact critical life history stages of marine organisms is a strategy for managing dredging globally (EPA 2001, Erftemeijer 2006). The main focus of these strategies has been on reproduction and recruitment of corals and fish (Ertemeijer et al 2012, Bridges 2010, Balazik 2012). Here we demonstrate that seagrasses have similar critical life history stages throughout the year and that these stages are distinct for our study area (Figure 6). In the current example, to manage the indirect impacts of dredging on nearshore beds of *Halophila decipiens*, operations during the wet period (November to April) would have little influence on critical life history stages. However, dredging through the dry period (May – October) would more likely impact these critical stages. Any activity during the dry period would need either careful management of light levels to maintain growth of *H. decipiens* meadows or risk the requirement for seagrass remediation and seed based restoration after the activity is completed. Similar management strategies are in place for port development in Darwin Harbour, Northern Territory where dredging only occurs during the wet period (Erfteimeijer, pers. comm. 2014) and in Gladstone Harbour, Queensland where a running average of available light for seagrass growth thresholds are used (Chartrand et al., 2012). Rasheed et al. (2014) and York et al. (2015) have furthered our understanding of seasonal abundances and recovery mechanisms of *Halophila spp.* in NE Australia. Together with our results, it is clear that ephemeral species with a transient seed bank, which move in both space and time (McMahon et al 2014), need to be managed for their whole life history. However, more intensive research efforts are required to characterize life history transitions and the ecological thresholds driving these transitions as quickly as possible given the development pressures already existing in tropical regions of Australia.

A species that transitions with change rather than resisting it will have inherent ecological advantages in highly disturbed environments but this transient nature creates difficulties for managing against environmental loss. *Halophila decipiens* in NW Australia persist through unfavourable conditions by transitioning through life history stages that are synchronous to natural disturbance regimes. Knowledge of the timing of these life stages, and the ecological thresholds that define them, can be used to better inform management decisions. Moreover, a better understanding of the physiological and environmental constraints on reproduction needs to lead to safeguarding of conditions favourable for reproductive success, which should be explicitly reflected in policy (Kilminster et al. 2015). Seagrasses are often managed using fixed reference levels (e.g. no net loss) at sites repeatedly visited over time (Marba et al., 2013). Seagrass ecosystems were managed this way as the importance of seeds for seagrass recovery has, until recently, received limited attention (Kendrick et al., 2012b), and most management plans were modelled on temperate seagrass species highly resistant to light deprivation (Gordon et al., 1994; Collier et al., 2009; McMahon et al., 2011). The use of reference sites and standing stock thresholds should be combined with methods that account for the ephemeral contribution of different life stages and a framework that emphasises vulnerability assessments of different life stages (Figure 6). As such, management strategies recognising the high temporal and spatial variability of these populations would need to be underpinned by adaptive rather than static management frameworks.

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Figure Captions

Figure 1: Grab and towed video sampling locations near James Price Point (north of Broome). Grey contour lines show 5 m changes in water depth. Inset shows the general survey area within the Kimberley region (hashed) in Western Australia.

Figure 2: Temporal and spatial patterns in seagrass biomass (A and B) and seed density (C and D) averaged over all sites **(± se, n= 60)**. Red underline shows samples taken during the dry period and blue the wet period.

Figure 3: Mean seagrass cover (± se, n = 4) estimated from images collected using a remotely operated vehicle (ROV).

Figure 4. Monthly averaged environmental conditions for the sites where data was collected.

Figure 5: *Halophila decipiens* life cycle adapted to environmental conditions in tropical NW Australia. % SI: Percent Surface Irradiance (reaching the seafloor). Values in brackets signify mean values

Figure 6: Conceptual model of *Halophila decipiens* life history. (A) is the ecological threshold for a change in state (habitat loss to habitat recovery) and for *Halophila* it is the environmental cue to seed germination; (B) is the ecological threshold for a change in state (habitat recovery to habitat loss) and for *Halophila* it is the loss of the adult population (standing stock) and dispersal of seeds via sediment transport; (C) denotes the life stage most

vulnerable to environmental perturbations due to the reliance on seeds to maintain species distribution through unfavourable conditions during the wet season and therefore the stage when direct anthropogenic disturbances (e.g. dredging) are restricted, either by imposing a water quality threshold or stopping activities until a minimum reproductive output is reached (this may be a minimum number of seeds in sediment grab sample based on historical seed densities).

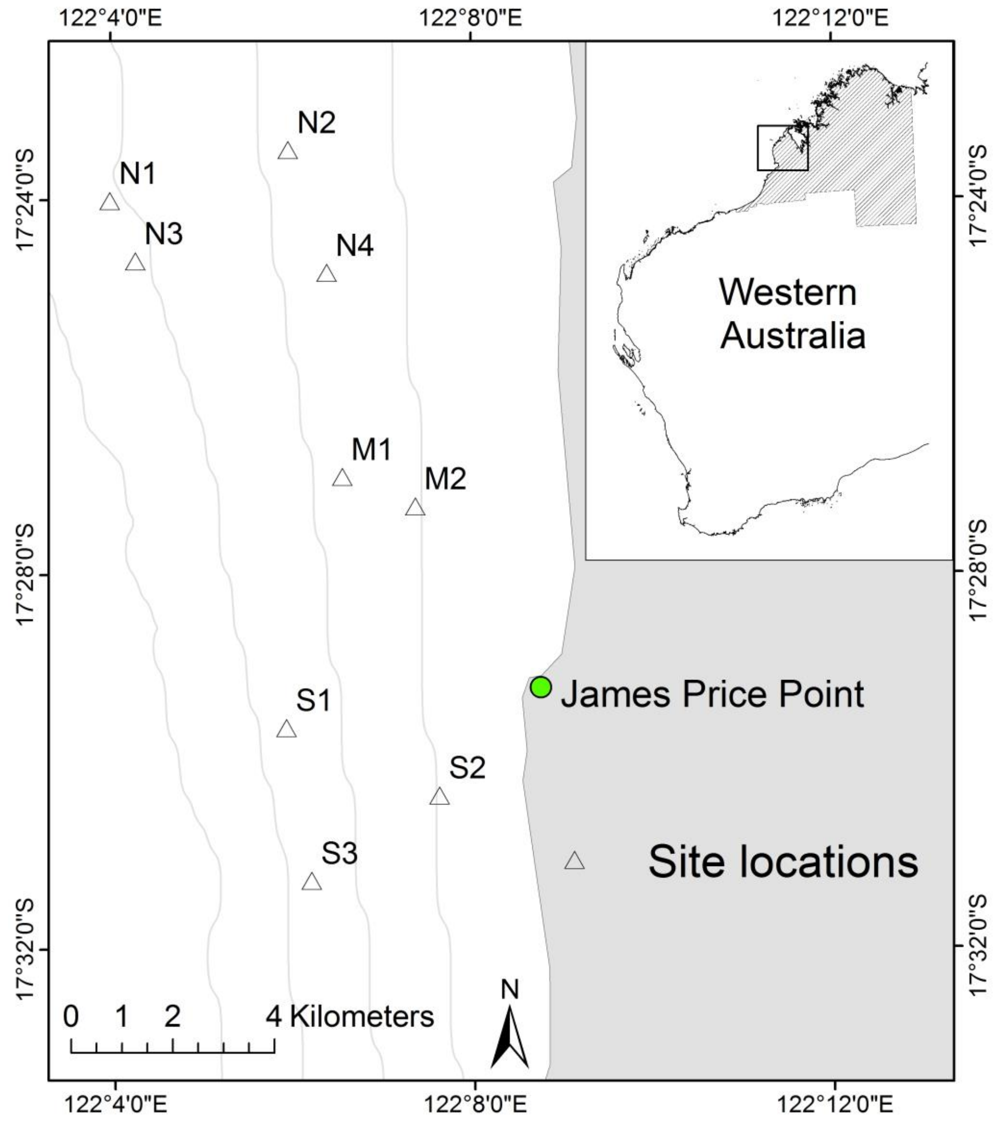
122°4'0"E
122°8'0"E
122°12'0"E
17°24'0"S
17°28'0"S
17°32'0"S
N1
N2
N3
N4
M1
M2
S1
S2
S3
James Price Point
Site locations
Western Australia
0 1 2 4 Kilometers
N

Figure 1:

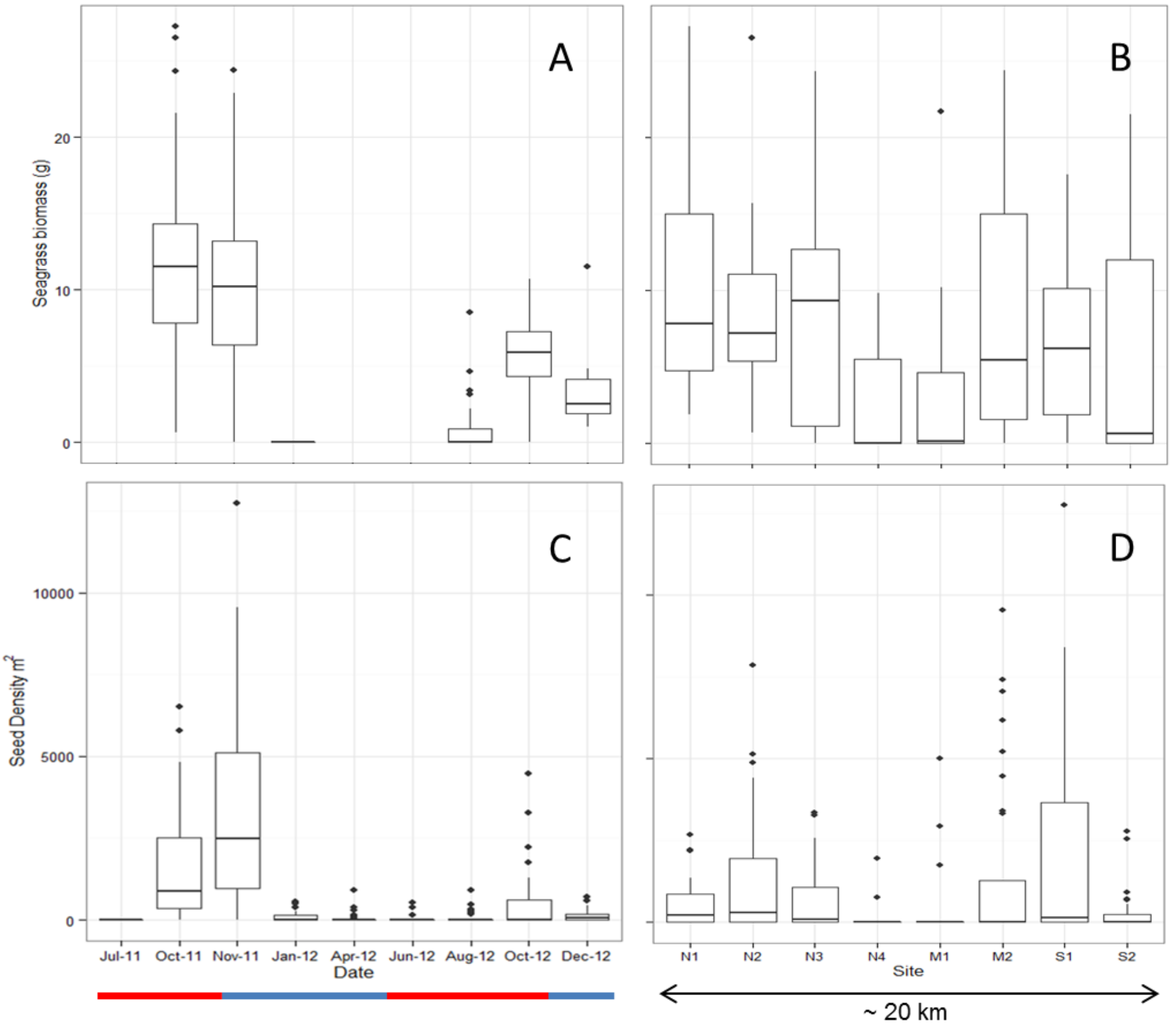
A
B
C
D
Seagrass biomass (g)
0
10
20
Seed Density m^2
0
5000
10000
Jul-11
Oct-11
Nov-11
Jan-12
Apr-12
Jun-12
Aug-12
Oct-12
Dec-12
Date
N1
N2
N3
N4
M1
M2
S1
S2
Site
~ 20 km

Figure 2:

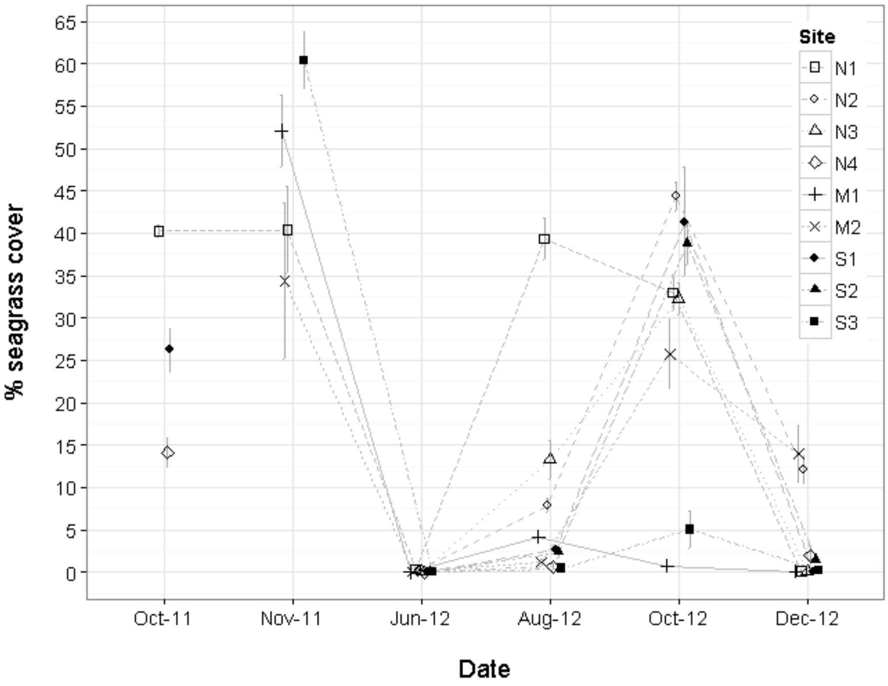
% seagrass cover
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Oct-11
Nov-11
Jun-12
Aug-12
Oct-12
Dec-12
Date
Site
N1
N2
N3
N4
M1
M2
S1
S2
S3

Figure 3:

Figure 4.

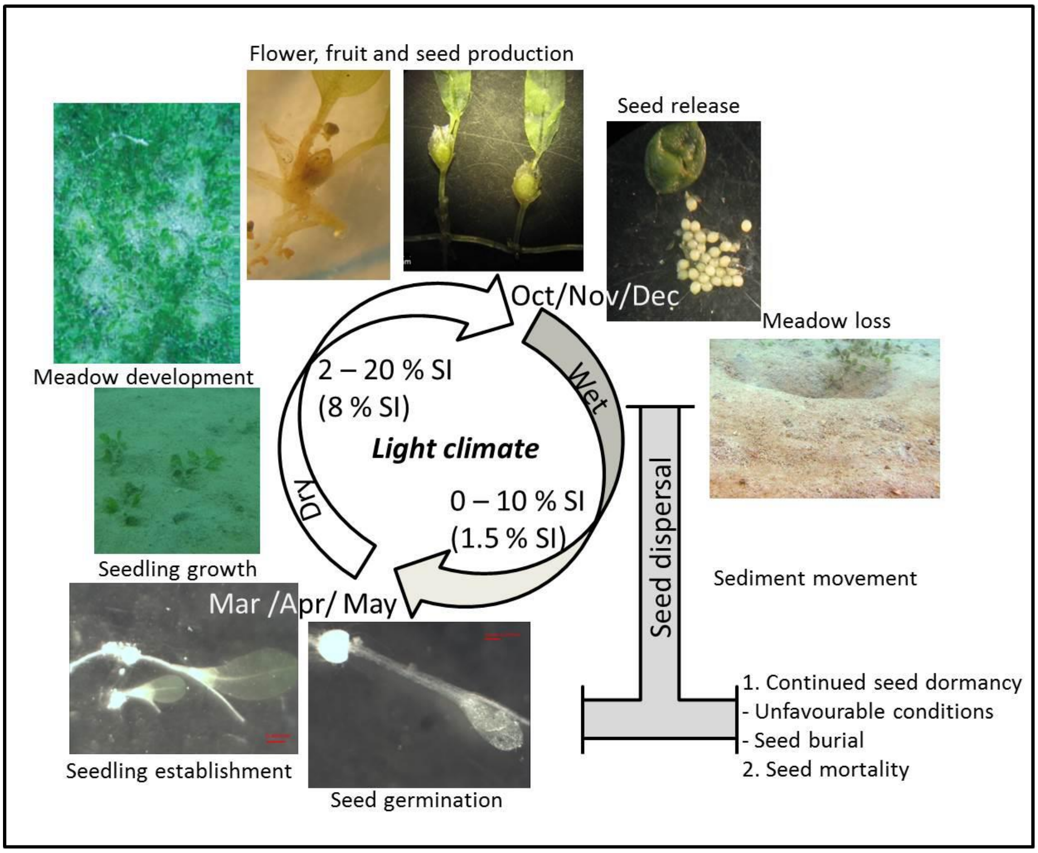
Flower, fruit and seed production
Seed release
Oct/Nov/Dec
Meadow loss
Meadow development
2 – 20 % SI
(8 % SI)
Wet
Light climate
Dry
0 – 10 % SI
(1.5 % SI)
Seed dispersal
Seedling growth
Sediment movement
Mar /Apr/ May
1. Continued seed dormancy
- Unfavourable conditions
- Seed burial
2. Seed mortality
Seedling establishment
Seed germination

Figure 5:

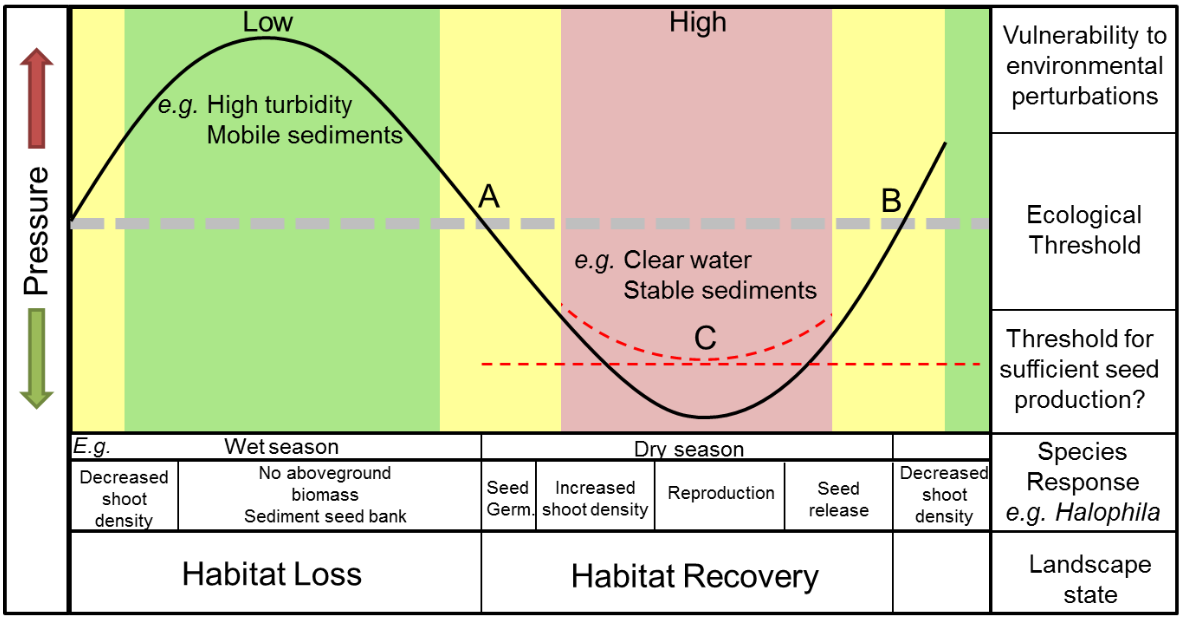
Pressure
Low
High
e.g. High turbidity
Mobile sediments
A
B
e.g. Clear water
Stable sediments
C
Vulnerability to environmental perturbations
Ecological Threshold
Threshold for sufficient seed production?
E.g.
Wet season
Dry season
Decreased shoot density
No aboveground biomass
Sediment seed bank
Seed Germ.
Increased shoot density
Reproduction
Seed release
Decreased shoot density
Species Response e.g. Halophila
Habitat Loss
Habitat Recovery
Landscape state

Figure 6:

Supplementary Material

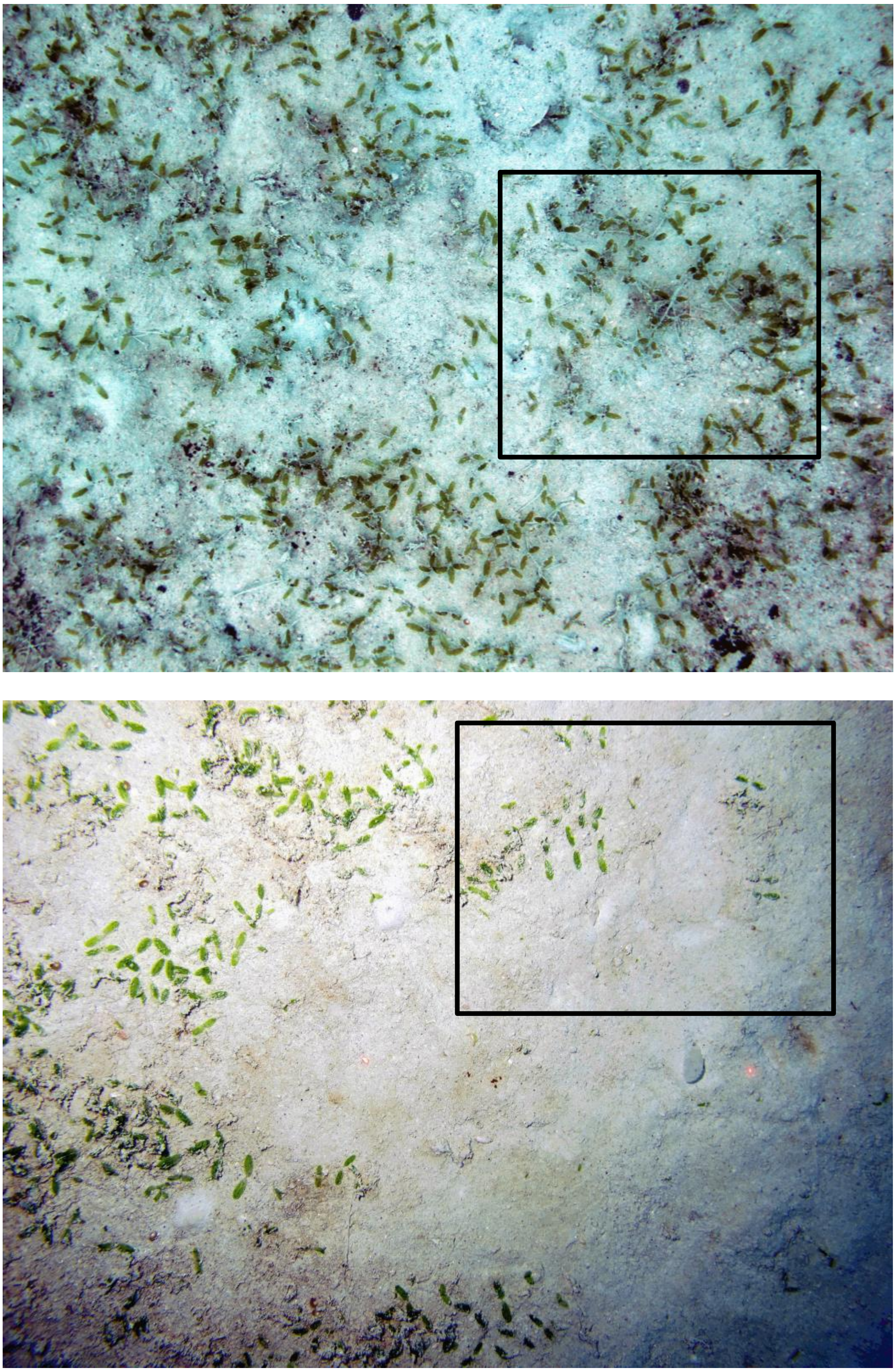

Figure 1: Examples of images taken from the ROV showing evidence of erosion (top) and deposition (bottom).