Managing Seagrass Resilience Under Cumulative Dredging Affecting Light: Predicting Risk Using Dynamic Bayesian Networks

Paul Pao-Yen Wu[a,b,g], Kathryn McMahon[c,d], Michael A. Rasheed[e], Gary A. Kendrick[c,f], Paul H. York[e], Kathryn Chartrand[e], M. Julian Caley[a,b], Kerrie Mengersen[a,b]

[a]*Australian Research Council Centre of Excellence in Mathematical and Statistical Frontiers*
[b]*School of Mathematical Sciences, Science and Engineering Faculty, Queensland University of Technology*
[c]*The Western Australian Marine Science Institution*
[d]*School of Natural Sciences, Edith Cowan University*
[e]*Centre for Tropical Water & Aquatic Ecosystem Research, James Cook University*
[f]*UWA Oceans Institute and School of Plant Biology, University of Western Australia*
[g]*Email: p.wu@qut.edu.au, Ph: 61 7 3138 9828, Fax: 61 7 3138 2310, GPO Box 2434, Brisbane QLD 4001.*
Co-author email addresses (in order): k.mcmahon@ecu.edu.au, michael.rasheed@jcu.edu.au,
gary.kendrick@uwa.edu.au, paul.york@jcu.edu.au, katie.chartrand@jcu.edu.au, julian.caley@gmail.com,
k.mengersen@qut.edu.au.

Running title (42 characters): Seagrass Resilience to Cumulative Dredging

Word count: 7109

Word count - summary: 348

Word count - main text: 4821

Word count - acknowledgements: 53

Word count - references: 1377

Word count - tables and figure legends: 510

Number of tables: 1

Number of figures: 4

Number of references: 54

Abstract

1. Coastal development is contributing to ongoing declines of ecosystems globally. Consequently, understanding the risks posed to these systems, and how they respond to successive disturbances, is paramount for their improved management. We study the cumulative impacts of maintenance dredging on seagrass ecosystems as an example of coastal development impacting marine ecosystems. Maintenance dredging causes disturbances lasting weeks to months, often repeated at yearly intervals.

2. We present a risk-based modelling framework for time varying complex systems centred around a Dynamic Bayesian Network (DBN). Our approach estimates the impact of a hazard on a system's response in terms of resistance, recovery and persistence, commonly used to characterise the resilience of a system. We consider whole-of-system interactions including: light reduction due to dredging (the hazard), the duration, frequency, and start time of dredging, and ecosystem characteristics such as the life history traits expressed by genera and local environmental conditions.

3. The impact on resilience of dredging disturbances is evaluated using a validated seagrass ecosystem DBN for meadows of the genera *Amphibolis* (Jurien Bay, WA, Australia), *Halophila* (Hay Point, Queensland, Australia) and *Zostera* (Gladstone, Queensland, Australia). These three genera encompass the range of seagrass life histories globally. Although impacts varied by combinations of dredging parameters and the seagrass meadows being studied, in general, 3 months duration or more, or repeat dredging every 3 years or more, were key thresholds beyond which resilience can be compromised. Additionally, managing light reduction to less than 50% can significantly decrease one or more of loss, recovery time and risk of local extinction, especially in the presence of cumulative stressors.

4. *Synthesis and application:* Our risk-based approach enables managers to develop thresholds for management by predicting the impact of different configurations of anthropogenic disturbances being managed. Many real-world maintenance dredging requirements fall within these parameters, and our results show that such dredging can be successfully managed to maintain healthy seagrass meadows in the absence of other disturbances. Here, we evaluated opportunities for risk mitigation using time windows; periods during which the impact of dredging stress did not impair resilience, especially for *Halophila* and *Zostera*.

2

1. Introduction

Globally, coastal development poses a significant threat to valuable ecosystems (Halpern et al., 2008). Coastal development is commonly associated with dredging, which presents a hazard to ecosystem health via stressors including light degradation and water quality reduction. Worldwide, hundreds of millions of cubic metres of sediment are dredged annually (Erftemeijer et al., 2006; IADC, 2014). This dredging is contributing to serious declines in primary producer ecosystems, including corals (Pandolfi et al., 2005), seagrasses (Waycott et al., 2009; Orth et al., 2006) and mangroves (Valiela et al., 2001). However, despite the need to manage and mitigate the effects of such disturbances, methods available to do so are severely limited (Carpenter et al., 2009).

Understanding cumulative impacts from a combination of stressors over time, such as repeated dredging events typical of maintenance dredging, is especially important (Crain et al., 2008). For example, widescale losses at Laguna Madre, Texas have been attributed to otherwise small-scale, routine maintneance dredging in 1965 and 1974 (Onuf, 1994). Yet, other long-term maintenance dredging programs have continued for decades with little evidence of seagrass decline, such as those in Gulf of Carpentaria in Australia (Rasheed and Unsworth, 2011; Unsworth et al., 2012). Methods for predicting how much these ecosystems are impacted and how they respond to stressors such as dredging, are an urgent priority to assist managers in formulating strategies to arrest these declines (Cote et al., 2016).

Resilience is a critical trait that underpins the successful management of complex ecosystems (Levin and Lubchenco, 2008; Holling, 1973). Although many definitions exist, we focus on ecological resilience (Angeler and Allen, 2016), which is centred around the set of processes and structures underpinning an ecosystem, and which incorporates estimations of ecosystem persistence including resistance to and recovery from stressor scenarios (Halpern et al., 2007; Hodgson et al., 2015). We also include a direct measure of persistence to characterise resilience, using the probability of local extinction (i.e. zero population over a relevant period of time). Resistance and recovery are them-

3

selves derived from the system response over time to natural and anthropogenic stressors. However, predicting this response is challenging as it emerges non-linearly from cumulative interactions of stressors, and environmental and ecological processes with different dynamics (Holling, 2001; Crain et al., 2008). In addition, there are significant uncertainties associated with biological systems, future environmental conditions that may support or impede their recovery, and our current understanding of the dynamics of complex ecosystems (Regan et al., 2002). Because of these high levels of variability and uncertainty in ecosystem states, dynamics and disturbance scenarios, it is impractical to predict responses solely from experiments. Whole-of-systems models that capture uncertainty are needed (Wu et al., 2017).

One systematic approach to managing complex systems under uncertainty is the risk framework, which has been applied widely in domains including environment, engineering and health (Kaplan and Garrick, 1981; Pate-Cornell, 1996). At its core, risk is a composite metric composed of the probability of a consequence, such as a fatality, and a scenario. Typically, the scenario comprises hazards and the causal sequence of events that precipitated these hazard states (Kaplan and Garrick, 1981). Such an approach could be used to assess resistance by modelling the probability of a certain level of loss immediately after the conclusion of a dredging campaign. However, recovery and persistence are more challenging to assess due to the uncertainty associated with future environmental conditions.

We developed a risk modelling approach based on a Bayesian Network (BN), a tool that has been applied with increasing frequency in ecology (Pearl, 1988; Korb and Nicholson, 2010; Pollino et al., 2007). BNs capture the conditional probabilistic relationships between system factors, and thus can capture interactions between different ecosystem processes and components. These relationships are represented both visually with a directed acyclic graph to support communication and collaboration, and quantitatively via conditional probabilities (Uusitalo, 2007; Pollino et al., 2007). They demonstrate good predictive accuracy even with limited data and can be parameterised using a combination of data and expert knowledge.

Most importantly, BNs directly represent and make inferences about risk, such as the risk of extinction, as they are a probabilisitic state space model. Risk scenarios are implemented by

4

setting observed system states as inputs, such as hazard states, which are referred to collectively as 'evidence'. The model then infers the posterior probability distribution from this evidence to predict the whole-of-system response to the specified risk scenario. BNs applied in ecology are predominantly static (Chee et al., 2016). However, resilience emerges from cumulative effects and feedback loops characteristic of complex biological systems (Grzegorczyk and Husmeier, 2011; Walker et al., 2004). Dynamic BNs (DBNs) extend BNs to enable the capture of feedback loops. They model the system at discrete points in time (time slices), which enables the accumulation of potentially non-linear interactive effects from one time slice to the next, similar to Markov models (Murphy, 2002; Chee et al., 2016).

BNs have been used to model seagrass ecosystems for a wide variety of decision support applications for management and policy making (e.g. Maxwell et al., 2015). These applications demonstrate the capability and flexibility of the approach for modelling interactions and uncertainty in a complex system (Levin and Lubchenco, 2008). Many of these models are constructed using expert elicitation and formulated at a high level to capture average effects across a broad array of stressors. They cannot capture emergent effects, or the impacts of timing, as BNs are time-aggregated models. Differential equation models of resilience can capture cumulative effects (e.g. Anthony et al., 2015) but are focused on scenario analysis without an explicit means for encoding uncertainty and thus synthesising risk. Specifically, although existing methods capture uncertainty in disturbances (e.g. Mumby et al., 2014), we go further to capture uncertainty explicitly in both ecosystem function and disturbance as enabled by the BN and DBN framework (Pearl, 1988). A DBN model focused on seagrass and dredging can potentially develop new insights through the capture of emergent cumulative effects. In addition, such a model could potentially be validated with greater confidence than a general, time-aggregated, high-level model.

We propose a scenario based DBN modelling approach based on the risk framework for predicting resilience. A review of existing work (Supporting Information Appendix ??) reveals opportunities for predicting resilience to stressors; we present our framework in Section 2. The case study of a seagrass dredging model is described (Section 2.1) and empirically validated (Supporting Information Appendix S2). We demonstrate the framework with this case study, focusing particularly

on the cumulative effects of regular maintenance dredging (Section 4). From these responses, we derive thresholds for dredging to support decision makers as part of a risk-informed management strategy.

2. Materials and Methods

Using the seagrass dredging case study (Section 2.1), we develop a framework (Section 2.2) for analysing resilience using DBNs.

2.1. Seagrass DBN and Dredging Case Study

Here we study periodic maintenance dredging as an example of cumulative impacts applied to seagrass meadows. We focus on the impact of light on seagrass ecosystems in terms of environmental baselines and as a key stressor arising from dredging. Light is a central driver of growth and physiology for seagrasses and other autotrophs (Kilminster et al., 2015). We consider impacts in terms of three different time periods: (i) the baseline time period T_B and corresponding population or ecosystem states against which we benchmark impacts, (ii) the period of active dredging, i.e. the hazard, T_H, and (iii) the consequence time period T_C where the dredge plume has ended but seagrass are potentially still affected. As maintenance dredging effects are typically localised, we assume that the period of active dredging is also approximately the duration of the dredge plume (Ports Australia, 2014; York et al., 2016).

We focus on the population response for assessing resilience to dredging stressors (Section 2.2). Given the growth dynamics of seagrass meadows (McMahon et al., 2013) and seasonal variations in their population and life histories (Kilminster et al., 2015), we adopt a monthly time scale and baseline period of 12 months (i.e. $T_B = \{$Jan,Feb,...,Dec$\}$, the length of T_B is $n_{T_B} = 12$). The consequence period was chosen as five years immediately following the hazard, $n_{T_C} = 60$ months and $T_C = \{$Jan-Year1,Feb-Year1,...,Dec-Year5$\}$ for a hazard ending in December. We adopted the Western Australia Environmental Protection Agency's regulatory framework for seagrass where a failure to recover within five years is considered permanent loss (Environmental Protection Agency, 2009). Under this formulation, recovery is chosen to be the time in months when the system first

6

returns to and stays within 20% of baseline population levels during the consequence period T_C. Resistance is the ratio of the population at the end of the last dredging period in T_H to the baseline population level, noting that there can be gaps between dredging periods for repeated maintenance dredging (e.g. $T_H = \{Jan - 2016, Feb - 2016, Jan - 2018, Feb - 2018\}$). Persistence here is the accumulated risk of zero population found by summing the probability of zero population over T_C (Supporting Information, Appendix S1).

We developed hazard scenarios that were combinations of each of the following dimensions:

- Dredging durations of 1, 2, 3 or 6 months (corresponding to consecutive time points in T_H),

- Frequency of maintenance dredging, from once off, to every 5, 3, 2 years and every year,

- Level of light stress during the dredging period $\delta(x^{\text{light}}_{\text{below sat.}}, T_H) = \{1, 0.75, 0.5, 0.25\}$,

- Month for commencement of dredging ranging from January to December,

giving a total of 960 hazard scenarios. We applied hierarchical models for light stress using as an approximation the number of days of above saturation light in that month (Section 2.3). Also, a 12 year simulation window was used to accommodate model initialisation (two years) and up to five-yearly maintenance dredging.

These scenarios were applied to the analysis of resilience for the following genera and locations: (i) *Amphibolis* at Jurien Bay, Australia, (ii) *Halophila* at Hay Point, Australia, and (iii) *Zostera* at Pelican Banks, Gladstone, Australia. These three genera exhibit the life history characteristics of each of the three major seagrass categories, namely, persistent, colonising and opportunistic, respectively (Kilminster et al., 2015). A meadow may be enduring, where seagrass are present all the time although population levels can vary, or transitory, where the population alternates between periods of absence and presence (Kilminster et al., 2015). Jurien Bay and Gladstone are enduring meadows whereas Hay Point is transitory. The baseline probability of above saturation light was encoded as $\delta(x^{\text{light}}_{\text{above sat.}}, t), t = \{\text{Jan, Feb,..., Dec}\}$. Note that $\delta(x^{\text{light}}_{\text{above sat.}}, t)$ can also represent the proportion of days of above saturation light in that month. Therefore, dredge durations of less than one month could be encoded by setting this parameter as the fraction of the month over which dredging occurred.

7

A DBN model of seagrass and dredging was developed and validated predominantly through expert elicitation (Fig. 1) (Wu et al., 2017). Although expert elicitation is widely used in existing seagrass models , the DBN can integrate expert knowledge and data in a dynamic, whole-of-systems model, overcoming limitations of existing data (Caley et al., 2014; Uusitalo, 2007). The DBN captured complex probabilistic relationships between factors and their impact on population, measured via shoot density and biomass. These factors were organised (Fig. 1) in terms of resistance (e.g. physiology), recovery (e.g. growth), site conditions (e.g. genera present), and environmental factors (e.g. light). The response of the system to cumulative disturbances arises from interactions between nodes cumulatively over time as governed by Conditional Probability Tables (CPTs) (for details, refer to Supporting Information Appendix S7), and risk scenarios. Hierarchical linear models were used to develop evidence for risk scenarios and for validating the model (Section 2.3).

Here, we focus on shoot density for our analysis of resilience, although the same model is used for biomass. This focus is made possible by defining population states as a percentage of a reference site (Section 2.3). Shoot density represents the number of shoots per m^2 in states of high, moderate, low or zero. The realised shoot density (i.e. measured shoot density) at time slice t is a function of loss and recovery rate in that time slice, adjusted by the baseline shoot density node. Not to be confused with baseline time periods, the baseline shoot density node is used to directly capture site-specific seasonal trends at a high level in addition to environmentally driven seasonal changes. Realised shoot density in turn drives potential loss and recovery at the next time slice. Loss in shoot density captures both natural mortality and light and water quality drivers for the dredging study. Despite the presence of environmental hazard states, loss is mitigated by the ability of the plants to resist the hazard, which is linked to the physiological status of the plants. Over time, the physiological status can also be affected by environmental stresses. Similarly, environmental stresses can affect recovery factors such as lateral growth and recruitment from seeds.

2.2. A DBN Framework for Modelling Resilience

Given the hazard and baseline environmental conditions, we use the DBN to infer the state probabilities for every node in the network during the consequence period T_C (Murphy, 2002).

8

We benchmark population measures such as shoot density or biomass response in the consequence
period T_C against the baseline period T_B (for details, refer to Supporting Information Appendix
S1). Therefore, we seek to estimate resilience by comparing the consequence probability trajectory
for shoot density $P(X_{\text{shoot density}}(T_C)|\boldsymbol{E})$ with the baseline $P(X_{\text{shoot density}}(T_B)|\boldsymbol{E})$. Here, $\boldsymbol{E}$ is the
input evidence, in this case, the genus, location type, and light conditions which vary over time
periods T_B, T_H and T_C. We used month of year to align T_C with T_B to accommodate for seasonal
variations of population in persistent or transitory seagrass meadows (Kilminster et al., 2015). In
practice, the baseline could be the same site prior to human disturbance, or a nearby undisturbed
reference site (ARMCANZ, 2000). Note that T_B needs to be of sufficient length to capture one cycle
of variation, and the length of T_C needs to be long enough to capture relevant recovery phenomena
and periodic variations.

We evaluate resistance, persistence and recovery using the following criteria and a benchmarking
function (Supporting Information Appendix S1):

$$B(P(X_{\text{shoot density}}(T_C)|\boldsymbol{E}), P(X_{\text{shoot density}}(T_B)|\boldsymbol{E})) = \frac{\sum \boldsymbol{w_\alpha} P(X_{\text{shoot density}}(T_C)|\boldsymbol{E})}{\sum \boldsymbol{w_\beta} P(X_{\text{shoot density}}(T_B)|\boldsymbol{E})} \quad (1)$$

where $\boldsymbol{w_\alpha}$ and $\boldsymbol{w_\beta}$ are weight vectors for the consequence and baseline shoot density responses
respectively.

1. Resistance is computed using the system state immediately after the last dredging period,
   prior to any recovery. Here, $T_C = \max{(T_H)}$, $w_\alpha = w_\beta = 1$, where T_B is the corresponding
   month of the year to T_C in the baseline.

2. Persistence is estimated as the accumulated probability of zero population during T_C com-
   pared to that during the corresponding baseline time period, i.e. $P(X_{\text{shoot density}}(T_C) =$
   zero state$|\boldsymbol{E})$. For example, if $T_C = \{$Feb-Year1,Mar-Year1,...,Jan-Year3$\}$, then we set $T_B =$
   $\{$Feb,Mar,...,Dec,Jan,...,Dec,Jan$\}$. For persistence, $\boldsymbol{w_\alpha} = \boldsymbol{w_\beta}$ are a vector of ones.

3. Recovery differs from persistence in that we are interested in the entire probability distribution
   over time, not just the zero state. Thus, $P(X_{\text{shoot density}}(T_C)|\boldsymbol{E})$ is a matrix with n_{T_C} rows
   and columns corresponding to states. We aggregate across columns first using a weighted sum

²³² (weighted mean equation, Wu et al., 2017), with weights $\boldsymbol{\alpha}, \boldsymbol{\beta}$ derived from state thresholds

²³³ (Section 2.3). The time t_R when the consequence to baseline ratio first approaches and remains

²³⁴ at one, is time to recovery.

2.3. Hierarchical Linear Models for Risk Scenarios

²³⁶ An important feature of DBNs for modelling whole-of-system responses is their modularity as

²³⁷ enabled through conditional independence assumptions encoded in the structure of the network

²³⁸ (Pearl, 1988). This means it is possible to interface other models as input and/or output to specific

²³⁹ node(s). Here, we describe the use of hierarchical linear models to capture baseline light conditions

²⁴⁰ for scenario analysis and for validation of predicted shoot density, biomass, physiological status and

²⁴¹ growth.

²⁴² The DBN is a state space model that provides a discrete representation over all factors in discrete

²⁴³ time steps. We defined shoot density and biomass states using thresholds based on a reference site,

²⁴⁴ similar to those used for decision making in water quality management guidelines (ARMCANZ,

²⁴⁵ 2000). These nodes had states of high, moderate, low and zero. We used 20% and 80% of the

²⁴⁶ reference site population (e.g. shoot density) as thresholds between the moderate and high, and

²⁴⁷ moderate and low states, respectively, in line with guidelines for 'moderate protection' assuming a

²⁴⁸ uniform distribution. Therefore, the outputs of the model in terms of probability of high, moderate,

²⁴⁹ low and zero shoot density correspond directly to the risk of meeting management guidelines in

²⁵⁰ terms of probability and consequence.

²⁵¹ We also applied expert elicited thresholds such as uniform thresholds between 0% and 100% for

²⁵² physiological status and 1 to 10% for slow, 11 to 30% for moderate and $> 30\%$ for fast lateral growth.

²⁵³ Given the complexity and uncertainty associated with marine ecosystems, discretisation can better

²⁵⁴ represent this uncertainty through a commensurate level of precision such as high, moderate, low

²⁵⁵ versus continuous measurements with many significant digits. Finally, discretisation can also be

²⁵⁶ used to enhance model portability by encoding the impact of that factor on the ecosystem. Light

²⁵⁷ is one such example.

²⁵⁸ Light is measured as moles of Photosynthetically Active Radiation (PAR), mols photons per

10

m^2 per day. It directly influences photosynthesis but also cascades to other factors in seagrass ecosystems such as physiological status and growth. The level of light corresponding to the onset of maximum photosynthetic rates is termed the saturating irradiance level (I_k) as further increases in light has minimal impact on the photosynthetic rate (Talling, 1957). This level varies by genera, temperature, season and photoacclimation to local conditions (Lee et al., 2007). For a given month, the probability of above saturation light thus captures environmental patterns relating to weather events such as storms or ice and the biological light requirement for the local meadow at that time of year. As a result, a separate model for light enables a portable DBN that can be applied to different sites globally.

We use a hierarchical linear model to transform data observations into state probabilities. There are two potential approaches: (i) count the number of occurrences of each state (defined with thresholds) at each time point, and directly model the state probability via a binomial or multinomial model (two, or more than two states, respectively), or (ii) model the data directly and find the area under the posterior density curve between thresholds to estimate the probability. In a Bayesian framework, the former approach estimates the mean probability and uncertainty around it (as captured by the posterior density) whilst the latter only calculates the mean. However, the former approach has lower precision if the number of observations at each time point is low; correspondingly, the latter is useful when there are many gaps in the data.

We applied the latter approach to light monitoring data due to the presence of large data gaps on the order of months. We used a simple log-linear mixed effects model, equations (2), of PAR $Y_{y,m,i_{y,m}}$ using time (month of the year m) with groupings by year y; $i_{y,m}$ indexes the replicate number of the observation for that year and month. The log transformed PAR $Y_{y,m,i_{y,m}}$ is assumed to be normally distributed with mean $\mu_{y,m}$ and precision τ (inverse of standard deviation). The posterior density for $\mu_{y,m}$ is then compared to the light saturation threshold for that particular meadow to determine the probability of above or below saturation light (Lee et al., 2007). Here, estimated light $\mu_{y,m}$ is a linear regression of periodic effects from the month of year m with coefficients β_{1y} and β_{2y}, and background light level (intercept term) β_{0y}. Vague normal priors were put on means and vague gamma and uniform priors on precision and standard deviation, respec-

tively. The Gibbs sampler was used to fit the model and convergence was checked by inspecting the posterior trace plots and autocorrelation plots.

$$\log(Y_{y,m,i_{y,m}}) \sim \mathcal{N}(\mu_{y,m}, \tau)$$

$$\log(\mu_{y,m}) = \beta_{0y} + \beta_{1y}\sin\left(\frac{\pi m}{6}\right) + \beta_{2y}\cos\left(\frac{\pi m}{6}\right)$$

$$\beta_{jy} \sim \mathcal{N}(\mu_{\beta_j}, \sigma_{\beta_j}^2), j = 0, 1, 2$$

$$\mu_{\beta_j} \sim \mathcal{N}(0, 1e-6), j = 0, 1, 2 \qquad (2)$$

$$\sigma_{\beta_j} \sim \mathcal{U}(0, 100), j = 0, 1, 2$$

$$\tau \sim \mathcal{G}(0.001, 0.001)$$

For shoot density, we used a multinomial model that captured seasonal trends and/or experimental design as we were interested in the estimated probability and its uncertainty, and not in inferring gaps in the data. We used light and shoot density data collected from shading experiments and long term monitoring programs to validate the predictions of the model. Here, counts $Y_{i,j}$ of the number of observations for experiment i for state j are modelled with a multinomial distribution $\mathcal{M}$. A long term observational study of dredging was used to validate model predictions for *Halophila* whereas experimental studies were used for *Amphibolis* and *Zostera* (Supporting Information Appendix S3).

3. Results

Given the DBN model and scenarios, we firstly validated the model empirically for each of the three main seagrass life histories expressed by genera and then analysed risk scenarios to better understand cumulative impacts. The model demonstrated very good accuracy with Mean Squared Errors (MSE) on the order of 0.03 in predicting changes in overall population and intermediary physiological and growth factors (Supporting Information Appendix S2). MSE provides an indication of the magnitude of the deviation between predicted and observed probability.

Using the validated model, we analysed the ecosystem response in terms of recovery, resistance and persistence criteria, Fig. 2, 3, and Supporting Information Fig. S7, respectively. The responses

demonstrated an increase in risk with increasing probability of below saturation accumulated light during dredging (i.e. light reduction), dredging frequency and duration that was tempered by time of dredging commencement, duration and life history (i.e. genus). Let us denote a window as a period of time when dredging can commence such that the impact on resilience satisfies management objectives (Suedel et al., 2008). Specifically, we applied the resilience criteria for recovery, resistance and persistence defined in Section 2.2. These windows shrunk considerably with increasing probability of below saturation light and dredge duration. Overall, increasing from 50% to 100% probability of below saturation light during dredging had a profound effect on recovery as indicated by a transition from predominantly short recovery times (yellow squares in Fig. 2) to long recovery time (red squares in Fig. 2) especially for dredge frequencies of three yearly or higher. Compare 50%-3-3 (predominantly yellow) to 75%-3-3 (less yellow) and 100%-3-3 (predominantly red) for example. Within each light reduction group (Fig. 2), a repeated pattern of increasingly shorter windows corresponded to longer dredging durations as demarked by gray lines. Within each duration band, windows decreased with increasing dredging frequency, showing a noticeable step change for three yearly or higher dredge frequencies.

We defined expert elicited objectives for resistance, recovery and persistence (Hodgson et al., 2015) to explore their interaction as part of a holistic assessment of seagrass meadow resilience in response to theoretical or modelled maintenance dredging scenarios. Resistance criterion 1 was satisfied if there was no more than a 20% change between the weighted mean response α and the baseline β (Section 2.2). Similarly, recovery criterion 2 was satisfied if $\boldsymbol{\alpha}$ converged to within 20% of $\boldsymbol{\beta}$ within six months. Finally, persistence criterion 3 was achieved if the risk of zero with dredging was less than 2.5% more than that without dredging. The overall score was defined and coloured as shown in Fig. 4: 4 if all criteria were satisfied (dark green), 3 for all except criteria three (light green), 2 only criteria two and three (orange), and 1 only criterion two (yellow), 0 for no criteria (red).

Generally, *Amphibolis* meadows showed substantially fewer opportunities to mitigate the impact of dredging stress on resilience using time windows compared to *Halophila* and *Zostera*. Instead, *Amphibolis* achieved resilience by resisting dredging stress (Fig. 4). This result, which is reflected in

13

the resistance and persistence responses, Fig. 3 and Supporting Information Fig. S7, respectively, accords with the high resistance and slower growth dynamics of this genus (Kilminster et al., 2015). A consequence of this was higher risk of extinction compared to baseline scenarios that were noticeably greater than that for *Halophila* and *Zostera* (Fig. S7).

By comparison, even with only 50% light reduction, *Halophila* meadows already showed time windows where resilience was impacted (Fig. 4) as characteristic of the low resistance of this genus. They were susceptible predominantly over the growth season but showed a rapid, if not totally unaffected, recovery response at other times (Fig. 2), especially during the senescent season which was a time of zero population. This pattern of windows reflects the strong demarcation of growth and senescent seasons for this genus which re-establishes from seed banks (Kilminster et al., 2015; Hovey et al., 2015) which are thought to be largely unaffected by light reduction impacts of dredging as the seeds are dormant and can persist for 1-2 years (Orth and Harwell, 2006).

Zostera has life history characteristics that are intermediate between *Amphibolis* and *Halophila* and this was borne out in the results (Kilminster et al., 2015). *Zostera* had similar patterns of windows to *Halophila* but demonstrated higher resistance (Fig. 3) and a greater ability to recover with longer windows for longer dredging durations (Fig. 2). They had higher risk of extinction compared to *Halophila* but lower than that for *Amphibolis* (Supporting Information Fig. S7).

4. Discussion

Given specific dredging configurations and resilience criteria results (Fig. 4), thresholds for resilience can be derived from dredge duration, level of light reduction, start time and dredge frequency (Table 1). Such thresholds can help inform the management and design of monitoring programs for seagrass meadows affected by maintenance dredging.

Less than or equal to three months of dredging contributed to resilient responses for all three genera (Table 1). This resilience was achieved by *Amphibolis* predominantly through resistance via physiological resistance, leading to windows that spanned the entire year (i.e. dredging can start any time). For *Halophila*, the window corresponded to the senescent season with zero population. On the other hand, *Zostera* was resistant with a year round window for 50% light reduction and

14

Table 1: Thresholds beyond which resilience is compromised based on dredge duration, frequency and light reduction for each genus. Also shown is the main type of resilience achieved (resistance or recovery), either generally, or within a time window (refer to Fig. 4).

Genera	Scenario	Duration (months)	Frequency (once/x years)	Light Reduction (%)	Type of Resilience
Amphibolis	100% light reduction	<3	<1/3	100	Generally resistant
Amphibolis	<100% light reduction	<=3	<=1/3	50, 75	Generally resistant
Halophila	50% light reduction	>=1	>=0	50	Resistant in window
Halophila	>50% light reduction	<=3	<=1/1	>=50	Resistant in window
Halophila	High Frequency	<=3	>=1/3	>=50	Resistant in window
Zostera	50% light reduction	<=3	<=1/1	50	Generally resistant
Zostera	>50% light reduction	<=3	<=1/3	>=50	Recovery potential in window
Zostera	Long Duration	>=3	<1/3	>=50	Recovery potential in window

demonstrated recovery potential in shorter windows for greater light reduction levels. Note that these were *Zostera muelleri* meadows of this species adapted to local low light conditions; other meadows may not show the same level of resistance.

Dredging at greater frequencies, especially more than or equal to once every three years, drastically affected the length of windows, demonstrating the impact of cumulative effects (Table 1). *Halophila* appears to have been the least affected, surviving even annual dredging, due to the senescent season of zero population and fast growth rates (green scores in Fig. 4). However, window lengths decreased significantly with frequency. This was similarly the case for *Zostera* except that not only do the window lengths decrease, they also change from a resistant response to one of recovery (green to yellow scores, respectively, in Fig. 4). Compared to *Halophila*, *Zostera* was more resilient to dreding of longer durations whereas *Halophila* was more resilient to higher frequencies. The former had longer windows whilst the latter had short windows. On the other hand, the effect of increasing frequency of dredging on slow growing *Amphibolis* appears to be a predominantly binary response of resistance (green scores, Fig. 4) or loss (red scores).

Actual maintenance dredging regimes at our modelled locations are generally well below the durations, frequencies and intensities that the model would suggest would be of concern to seagrasses (Table 1). In addition, maintenance dredging plumes are often localised to small areas close to operations (Ports Australia, 2014; York et al., 2016). At Hay Point for example maintenance dredging has only occurred twice (in 2008 and 2010) since channels were established in 2006 with a duration of approximately 4 days on each occasion. For ports in Cairns and Townsville, maintenance dredging is annual but its duration is typically less than 4 weeks (Ports Australia, 2014). This is similarly the case in Western Australia. Dredging of one to four weeks duration could be approximated in this model by a one month duration with 25% to 100% light reduction level, respectively. In these scenarios, all three genera were mostly resilient assuming a return to baseline conditions post-dredging. However, window effects already come into play for three yearly or more frequent dredging for *Halophila* at 50% light reduction (i.e. two weeks dredging).

These results suggest that many existing maintenance dredging regimes already occur in ways that avoid some long term cumulative impacts to seagrass meadows and supports results from long

term seagrass monitoring that has been conducted in Australian ports with maintenance dredging requirements (Rasheed and Unsworth, 2011; Unsworth et al., 2012; McKenna et al., 2015; Coles et al., 2015). However, where maintenance dredging occurs over longer durations tending towards one month or more, or with increased frequencies and a greater potential to significantly reduce light, the application of appropriate windows developed in this model would provide a useful tool to manage dredging. In addition, maintenance dredging of short durations still has the potential to impact seagrasses especially where other non-dredging impacts, such as severe weather events have already occurred and acted to reduce meadow resilience prior to dredging activity (McKenna et al., 2015). This is an area for future research.

In addition, our model focused on light based impacts. The approach of using probability of above or below saturation light as a key input and driver of the model is advantageous in that it inherently accounts for local light adaptation as the light saturation threshold can vary across meadows of the same genus. However, knowledge of the saturation threshold for the local meadow is required. Ways to estimate this in the absence of such data would support the widespread application of our approach. Additionally, the specification of probability of above saturation light as an input enables the analysis of impact on individual meadows located in different areas relative to a dredge. Combining our approach with relevant hydrodynamic and/or plume models could also help to customise its application in a spatially explicit context. Furthermore, although nodes for connectivity due to seed or vegetative fragments were included (Fig. 1), connectivity is currently poorly understood for seagrass ecosystems and their impact on resilience could be explored as new data becomes available (Grech et al., 2016). Finally, other disturbance regimes such as those related to sediment burial or sediment quality effects could also be explored.

5. Conclusion

In light of the complex nature of ecosystems and their ongoing declines worldwide, our risk-based DBN modelling approach provides an opportunity for better management. The framework explicitly captures risk vis a vis hazard, probability and consequence over time given interactions and cumulative effects between biological and environmental processes, and successive disturbances.

17

The approach quantifies, using risk and ecosystem baselines as a benchmark, the response of the ecosystem in terms of resistance, recovery and persistence, the components of resilience. It had good predictive accuracy with a MSE on the order of 0.01 to 0.05 in the predicted probability distribution using empirical data across three representative genera. When applied to the maintenance dredging case study for seagrass, the risk model revealed that a dredging frequency greater than once every three years for durations of three months or less emerged as a key threshold beyond which resilience was compromised across the range of life histories. Both timing of dredging commencement and management of light reduction to less than 50% emerged as tools for mitigating one or more of loss, recovery time and risk of local extinction.

The application of this framework to other datasets, disturbance types, and biological communities has the capacity to reveal broad insights into how to manage for lower impact and greater resilience across different life histories, population types and dynamics and even the effect of predicted changes in background environmental conditions. Already our approach has revealed that some maintenance dredging scenarios currently in operation are likely to be appropriate (assuming no significant further disturbances outside baseline frequencies and probabilities) in terms of providing adequate opportunities for maintenance of seagrass communities as well as defining limits where application of windows would be of assistance.

6. Author Contributions

MJ Caley initiated the study, PP Wu and K Mengersen designed the methodology; K McMahon, M Rasheed, GA Kendrick, PH York and K Chartrand provided data, expert knowledge and ecological analysis; PP Wu developed and validated the statistical models; PP Wu led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

7. Acknowledgements

and assisted by seagrass and light data from Gladstone Ports Corporation (Gladstone) and North
Queensland Bulk Ports Corporation (Hay Point).

8. Data Accessibility

Data is provided in supporting information.

9. References

Angeler, D. G., Allen, C. R., 2016. Editorial: quantifying resilience. Journal of Applied Ecology 53 (3), 617–624.

Anthony, K., Marshall, P. A., et al., 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. Global Change Biology 21 (1), 48–61.

ARMCANZ, A., 2000. Australian and New Zealand guidelines for fresh and marine water quality. Australian and New Zealand Environment and Conservation Council and Agriculture and Resource Management Council of Australia and New Zealand, Canberra, 1–103.

Caley, M. J., O'Leary, R. A., et al., 2014. What is an expert? a systems perspective on expertise. Ecology and evolution 4 (3), 231–242.

Carpenter, S. R., Mooney, H. A., et al., 2009. Science for managing ecosystem services: Beyond the millennium ecosystem assessment. Proceedings of the National Academy of Sciences 106 (5), 1305–1312.

Chartrand, K. M., Bryant, C. V., et al., 2016. Light thresholds to prevent dredging impacts on the great barrier reef seagrass, *Zostera muelleri ssp. capricorni*. Frontiers in Marine Science 3, 106.

Chee, Y. E., Wilkinson, L., et al., 2016. Modelling spatial and temporal changes with GIS and spatial and dynamic bayesian networks. Environmental Modelling and Software 82, 108–120.

Coles, R. G., Rasheed, M. A., et al., 2015. The Great Barrier Reef world heritage area seagrasses: managing this iconic Australian ecosystem resource for the future. Estuarine, Coastal and Shelf Science 153, A1–A12.

Cote, I. M., Darling, E. S., et al., 2016. Interactions among ecosystem stressors and their importance in conservation. In: Proceedings of the Royal Society of London B: Biological Sciences. Vol. 283. p. 20152592.

Crain, C. M., Kroeker, K., et al., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11 (12), 1304–1315.

Environmental Protection Agency, December 2009 2009. Environmental assessment guidelines: No. 3 protection of benthic primary producer habitats in western australia's marine environment. Report, Western Australia.

Erftemeijer, P. L., Lewis III, R., et al., 2006. Environmental impacts of dredging on seagrasses: A review. Marine Pollution Bulletin 52 (12), 1553–1572.

Grech, A., Wolter, J., et al., 2016. Spatial patterns of seagrass dispersal and settlement. Diversity and Distributions 22 (11), 1150–1162.

Grzegorczyk, M., Husmeier, D., 2011. Non-homogeneous dynamic bayesian networks for continuous data. Machine Learning 83 (3), 355–419.

Halpern, B. S., Selkoe, K. A., et al., 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conservation Biology 21 (5), 1301–1315.

Halpern, B. S., Walbridge, S., et al., 2008. A global map of human impact on marine ecosystems. Science 319 (5865), 948–952.

Hodgson, D., McDonald, J. L., et al., 2015. What do you mean, resilient? Trends in Ecology and Evolution 30 (9), 503–506.

Holling, C. S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4 (1), 1–23.

Holling, C. S., 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4 (5), 390–405.

Hovey, R. K., Statton, J., et al., 2015. Strategy for assessing impacts in ephemeral tropical seagrasses. Marine pollution bulletin 101 (2), 594–599.

IADC, 23 Dec 2015 2014. Dredging in figures 2014. Report, International Association of Dredging Companies.

Kaplan, S., Garrick, B. J., 1981. On the quantitative definition of risk. Risk Analysis 1 (1), 11–27.

Kilminster, K., McMahon, K., et al., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. Science of the Total Environment 534, 97–109.

Korb, K. B., Nicholson, A. E., 2010. Bayesian Artificial Intelligence, Second Edition. CRC Press, Inc.

Lavery, P., McMahon, K., et al., 2009. Interactive effects of timing, intensity and duration of experimental shading on amphibolis griffithii. Marine Ecology, 21.

Lee, K.-S., Park, S. R., et al., 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: a review. Journal of Experimental Marine Biology and Ecology 350 (1), 144–175.

Levin, S. A., Lubchenco, J., 2008. Resilience, robustness, and marine ecosystem-based management. BioScience 58 (1), 27–32.

Maxwell, P. S., Pitt, K. A., et al., 2015. Identifying habitats at risk: simple models can reveal complex ecosystem dynamics. Ecological Applications 25 (2), 573–587.

McKenna, S., Jarvis, J., et al., 2015. Declines of seagrasses in a tropical harbour, north Queensland, Australia, are not the result of a single event. Journal of Biosciences 40 (2), 389–398.

McMahon, K., Collier, C., et al., 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecological Indicators 30, 7–15.

McMahon, K., Lavery, P. S., et al., 2011. Recovery from the impact of light reduction on the seagrass *Amphibolis griffithii*, insights for dredging management. Marine Pollution Bulletin 62 (2), 270–283.

Mumby, P. J., Wolff, N. H., et al., 2014. Operationalizing the resilience of coral reefs in an era of climate change. Conservation Letters 7 (3), 176–187.

Murphy, K. P., 2002. Dynamic bayesian networks: representation, inference and learning. Thesis.

Onuf, C. P., 1994. Seagrasses, dredging and light in Laguna Madre, Texas, U.S.A. Estuarine, Coastal and Shelf Science 39 (1), 75–91.

Orth, R. J., Carruthers, T. J., et al., 2006. A global crisis for seagrass ecosystems. Bioscience 56 (12), 987–996.

Orth, R. J., Harwell, M. C., 2006. Ecology of Seagrass Seeds and Seagrass Dispersal Processes. Springer Netherlands, Dordrecht, pp. 111–133.

Pandolfi, J., Jackson, J. B. C., et al., 2005. Are us coral reefs on the slippery slope to slime? Science 307 (5716), 1725–1726.

Pate-Cornell, M. E., 1996. Uncertainties in risk analysis: Six levels of treatment. Reliability Engineering and System Safety 54, 95–111.

Pearl, J., 1988. Probabilistic Reasoning in Intelligent Systems. Morgan Kaufmann.

Pollino, C. A., Woodberry, O., et al., 2007. Parameterisation and evaluation of a bayesian network for use in an ecological risk assessment. Environmental Modelling and Software 22 (8), 1140–1152.

Ports Australia, 2014. Dredging and australian ports: Subtropical and tropical ports. Report, Ports Australia, Sydney, NSW.

Rasheed, M. A., Unsworth, R. K., 2011. Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. Marine Ecology Progress Series 422, 93–103.

22

Regan, H. M., Colyvan, M., et al., 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological Applications 12 (2), 618–628.

Suedel, B. C., Kim, J., et al., 2008. A risk-informed decision framework for setting environmental windows for dredging projects. Science of The Total Environment 403 (13), 1–11.

Talling, J., 1957. The phytoplankton population as a compound photosynthetic system. New phytologist 56 (2), 133–149.

Unsworth, R. K., Rasheed, M. A., et al., 2012. Solar radiation and tidal exposure as environmental drivers of *Enhalus acoroides* dominated seagrass meadows. PloS one 7 (3), e34133.

Uusitalo, L., 2007. Advantages and challenges of bayesian networks in environmental modelling. Ecological Modelling 203 (3), 312–318.

Valiela, I., Bowen, J. L., et al., 2001. Mangrove forests: One of the world's threatened major tropical environments at least 35% of the area of mangrove forests has been lost in the past two decades, losses that exceed those for tropical rain forests and coral reefs, two other well-known threatened environments. Bioscience 51 (10), 807–815.

Walker, B., Holling, C. S., et al., 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9 (2), 5.

Waycott, M., Duarte, C. M., et al., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci 106 (30), 12377–12381.

Wu, P. P.-Y., Mengersen, K., et al., 2015. Predicting the temporal response of seagrass meadows to dredging using dynamic Bayesian networks. In: MODSIM2015 21st Int. Congress on Modelling and Simulation. MSSANZ, pp. 1282–1288.

Wu, P. P.-Y., Mengersen, K., et al., 2017. Timing anthropogenic stressors to mitigate their impact on marine ecosystem resilience. Nature Communications In revision.

York, P., Reason, C., et al., 2016. Seagrass habitat of Cairns Harbour and Trinity Inlet: Annual monitoring report 2015. Report Publication 16/13, Centre for Tropical Water and Aquatic Ecosystem Research, JCU.

York, P. H., Carter, A. B., et al., 2015. Dynamics of a deep-water seagrass population on the Great Barrier Reef: annual occurrence and response to a major dredging program. Scientific Reports 5:13167.

(a) Overall network

(b) Resistance subnetwork

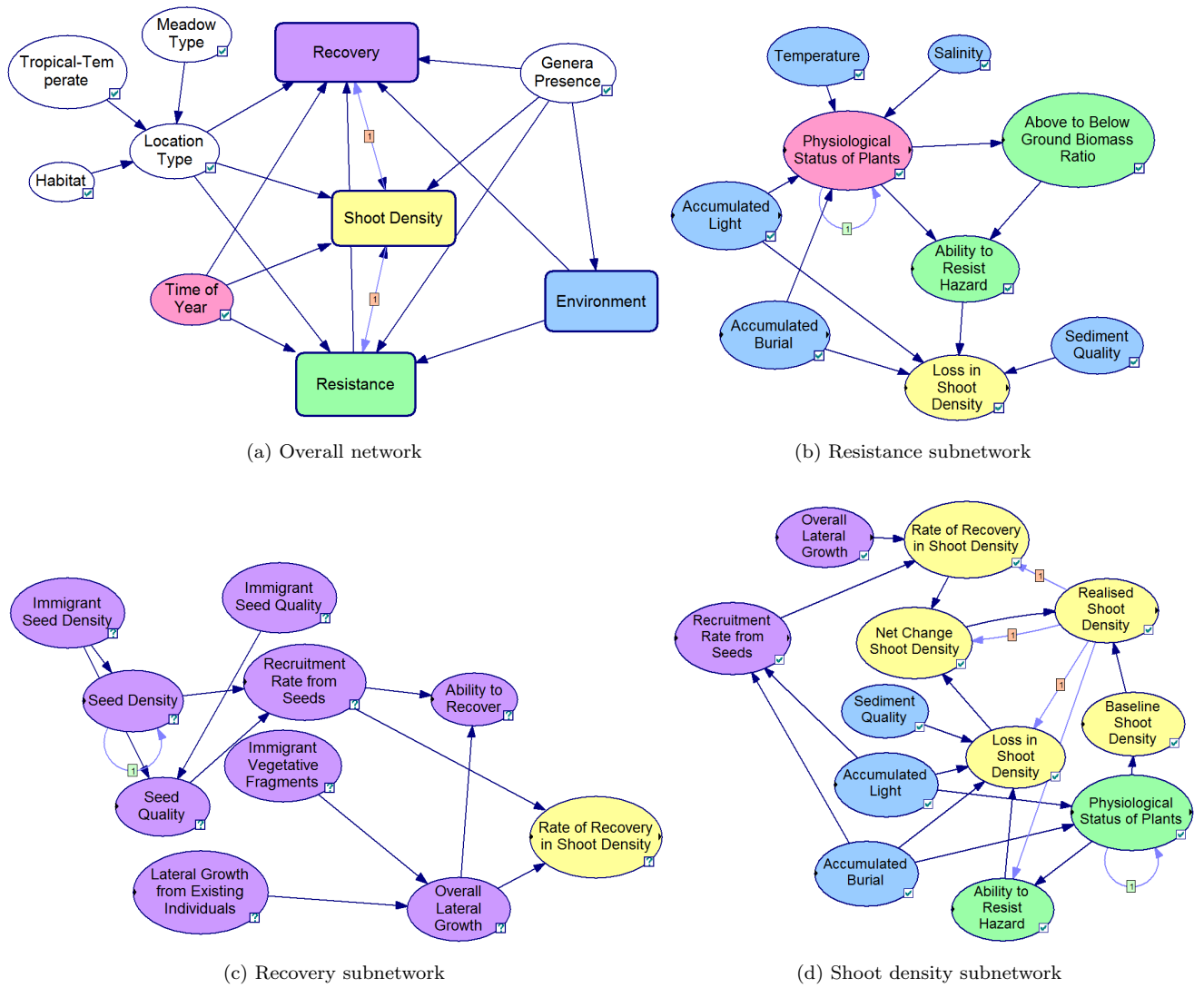(c) Recovery subnetwork

(d) Shoot density subnetwork

Figure 1: Illustration of overall seagrass DBN model (Wu et al., 2017) focusing on Shoot Density for clarity (Fig. 1a). Nodes are ovals and arrows denote conditional dependence between a parent and child node in the same time slice. Where an arrow is labelled with a 1, the child node is in the next time slice. Rounded rectangles denote subnetworks. Yellow nodes relate to loss and recovery in shoot density, purple nodes to recovery, green nodes to resistance, blue nodes to environmental factors X_e and pink for all other nodes. Biomass nodes, not shown, are connected in exactly the same way as the yellow shoot density nodes.
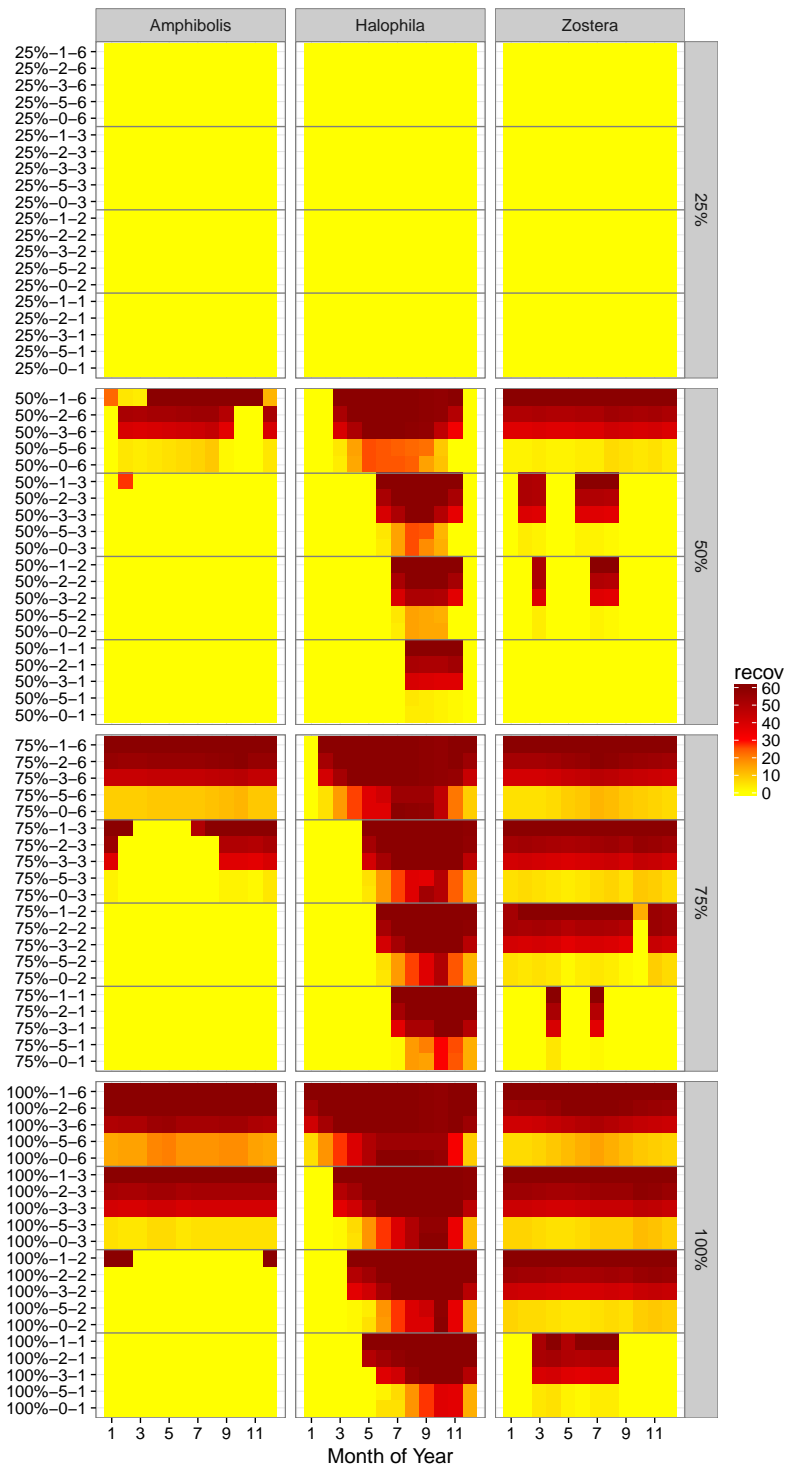
Figure 2: Expected recovery time in months for seagras genera *Amphibolis*, *Halophila* and *Zostera* (panels left to right) for different maintenance dredging hazard scenarios. The 12 columns in each panel correspond to dredging starting in Jan. through Dec. to assess the impacts of seasonality of dredging. Each row corresponds to a specific dredging light stressor scenario. Overall, they are grouped by light reduction level (100% light reduction equates to no light during dredging, 75%, 50% and 25% reduction), then by frequency of dredging (every year, 2, 3 or 5 years, or once off 0 years), and finally by dredging duration of 6, 3, 2, 1 month.
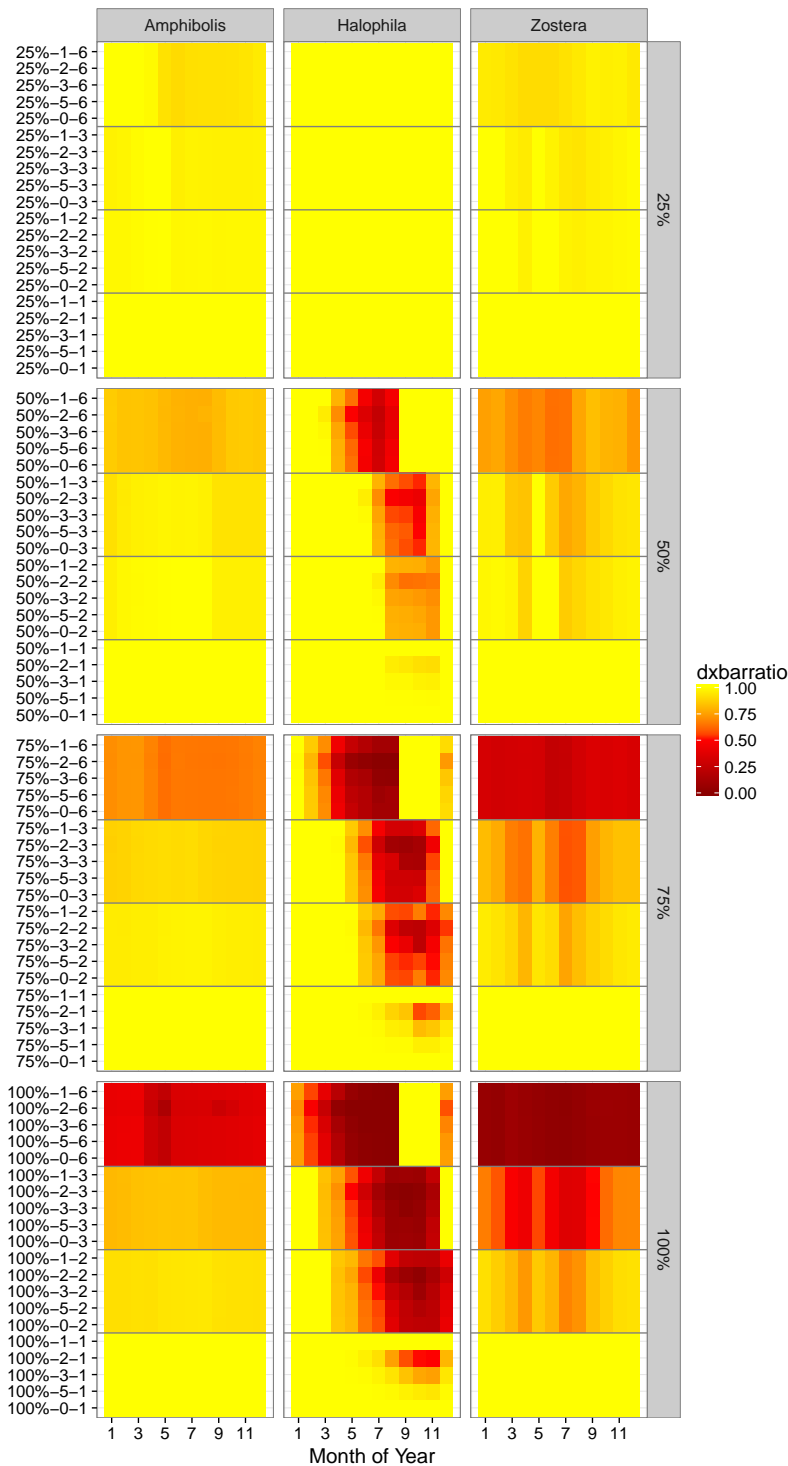
Figure 3: Resistance as ratio of baseline population immediately following dredging for seagrass genera *Amphibolis*, *Halophila* and *Zostera* (panels left to right) for different dredging hazard scenarios. There are 12 columns in each panel corresponding to dredging starting in Jan. through Dec. to assess the impacts of the seasonality of dredging. Each row corresponds to a specific dredging light stressor scenario. Overall, they are grouped by light reduction level (100% light reduction equates to no light during dredging, 75%, 50% and 25% reduction), then by frequency of dredging (every year, 2, 3 or 5 years, or once off 0 years), and finally by dredging duration of 6, 3, 2, 1 month.
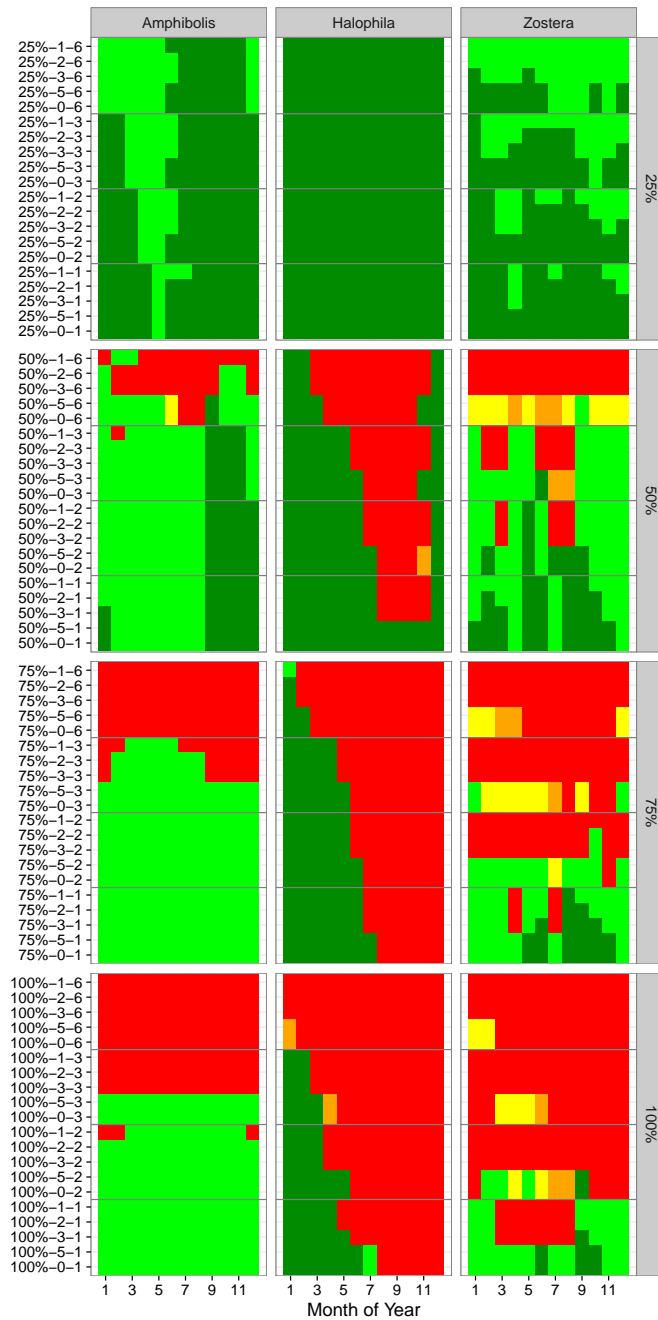
Figure 4: Risk-based resilience scores for seagrass genera *Amphibolis*, *Halophila* and *Zostera* (panels left to right) for different maintenance dredging hazard scenarios. The 12 columns in each panel correspond to dredging starting in Jan. through Dec. to assess the impacts of the seasonality of dredging. Each row corresponds to a specific dredging light stressor scenario. Overall, they are grouped by light reduction level (100% light reduction is no light during dredging, 75%, 50% and 25% reduction), then by frequency of dredging (every year, 2, 3 or 5 years, or once off 0 years), and finally by dredging duration of 6, 3, 2, 1 month. The bottommost row is the no dredging scenario. The colour of the cell describes the resilience criteria score for (1) resistance, (2) recovery and (3) persistence criteria where dark green represents all criteria satisfied, light green for criteria 1 and 2, orange for criteria 2 and 3, and yellow for just criteria 3. Red denotes no criteria satisfied.