Species Response Curves for Seagrass

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Type: Method

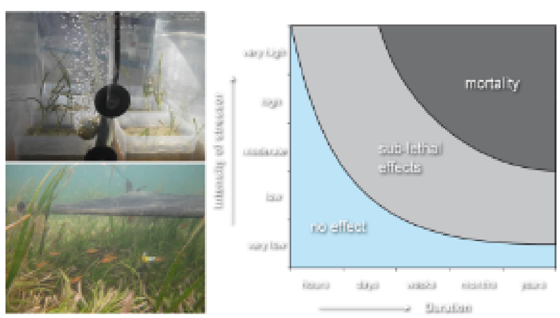
Project Phase: Initiation, Planning and Design

Purpose: Identifying tolerance levels of species to assess environmental impact from interventions

Requirements: Field and laboratory experience, ecological knowledge and analytical skills

Relevant Software: Statistical programme (eg. R)

About



This tool explains in general terms how seagrass responds to environmental conditions, specifically to reduced light penetration, which is one of the most severe threats for seagrass ecosystems worldwide. Such information is especially useful if planned infrastructural developments are expected to lead to (temporary) changes in environmental conditions in nearby sensitive ecosystems, e.g. dredging operations near coral reefs, mangrove forests or seagrass beds. The tool may give information on negative ecological impacts that may be expected from infrastructural developments, when and to what extent these impacts are expected to occur, to what extent negative impacts are reversible, and when managers, planners and constructors are to take precautionary measures to prevent irreversible damage. Information is provided on how to develop species response curves using lab and field experiments, and is therefore transferable to other species.

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Theoretical background

A species response curve typically describes the performance of a species in response to a gradient of a single abiotic environmental factor (Fig 1). These curves often, but not necessarily always, show an upper and lower limit for the persistence of a species and a range of conditions where the species have a good and optimal performance. Thus, a species response curve will typically describe under which conditions a species will be absent or can be present (i.e., referred to as niche width or tolerance), and if the species can be present, which densities the species may reach given the value of that specific environmental setting.

Environmental parameters

In the natural environment, there are of course a range of abiotic environmental factors for which a species will have a species-specific response curve. The actual abundance of a species will be determined by the environmental factor which has the most restricting value on the species response curve (i.e., the limiting factor). As soon as the condition of the limiting factor changes, the abundance of the species will change and stabilise at a new equilibrium. Depending on the species, abundance may be defined as (areal) biomass, (areal) number of individuals, shoot density, leaf density, etc.

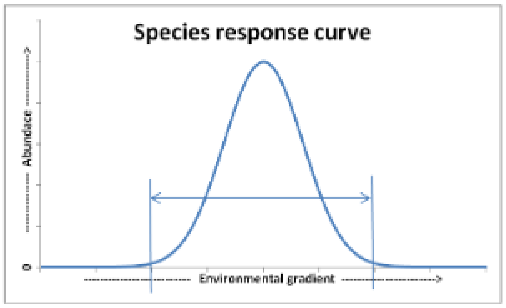

Fig. 1: Theoretical example of a Gaussian shaped species response curve.

In general, the closer an environmental parameter is to the species' upper or lower tolerance limits, the more stressful this is. Although a single limiting factor may restrict a species occurrence, it is too simple to see all abiotic factors as fully independent. The value of one variable, especially if it is close to a species' tolerance limit, may also have a limiting effect on the niche width or optimum value of another environmental parameter. E.g. the temperature niche width of seagrasses decreases with reducing light availability, because the energy consumption via respiration is higher at higher temperatures, while the energy production needed to maintain this higher respiration is lower at lower light intensity. Due to these kind of interactions between environmental parameters, the actual species response curve for a specific environmental variable may differ between locations.

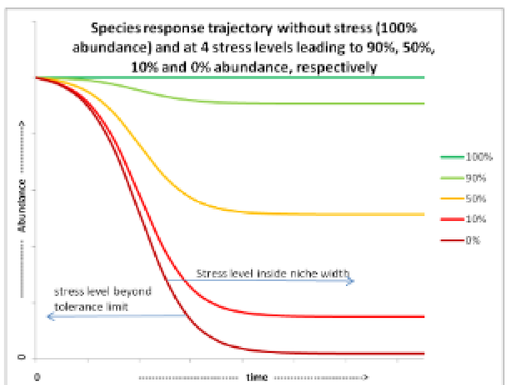

Fig.2:Conceptual development of species abundance over time in % of t=0 (optimal) abundance under optimal and sub-optimal environmental conditions.

Species response and species trajectory curves

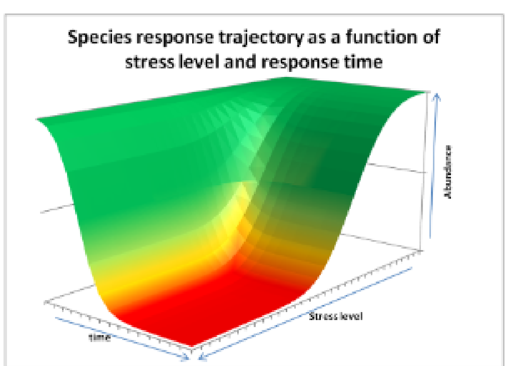

Fig.3:Conceptual 3D representation of species abundance as a function of species response

time in relation to stress level, defined as being exposed to sub-optimal environmental conditions.

The above-described Gaussian shaped species response curve is static in that it does not explicitly address temporal aspects about i) temporal variability in environmental conditions, ii) how long species can tolerate conditions outside the average tolerance limits and iii) the time required for a species to adjust to changing conditions. This makes it difficult to use a species response curve to derive the impact of temporal variability in abiotic conditions on a species performance. Short-term exceedance of average tolerance limits may however occur regularly e.g. due to temporal natural environmental variability. Species can have mechanisms to overcome conditions that exceed their average tolerance limits, but the dynamics of these mechanisms do not necessarily match up with the temporal variability causing the exceedance of average tolerance limits. The impact of exceeding tolerance limits has been related to the intensity, duration and frequency of the occurrence of environmental parameter(s) (e.g., for corals see Newcombe and MacDonald, 1991; McArthur et al., 2002). Therefore, an alternative to describe a species response to an environmental factor, is to plot a species response trajectory curve. A species response trajectory shows species abundance as a function of time under a specific environmental condition. Fig. 2 illustrates this for different stress levels.

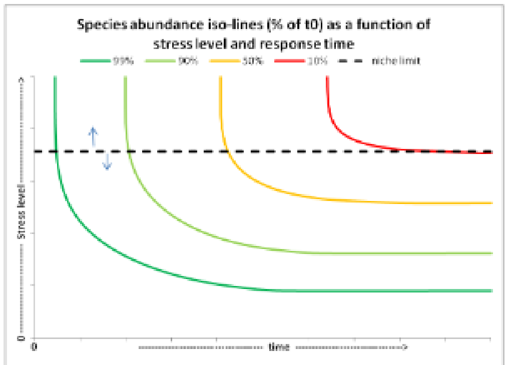

Fig.4:Conceptual result of expected species response based on a measurable stressor adapted from Erftemeijer et al., 2012).

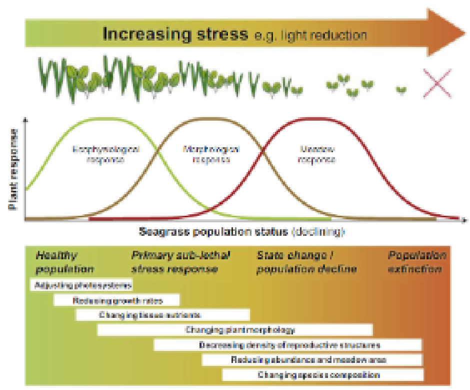

Fig.5: The model of seagrass' response towards light deprivation as a function of deprivation duration showing cascading coping mechanisms of 1st physiological, 2nd morphological and 3rd ecosystem and community level adaptations (Collier et.al., 2011).

Maintaining a 'stress' level corresponding with the environmental parameter value at which the occurrence of a species is optimal (indicated by the dark green 100% line in Fig. 2) does not lead to changes in abundance relative to t=0. If environmental factors change to a stress level beyond a species' tolerance limit, this will lead to 0% abundance over time (dark red 0% line in Fig 2). However, as long as a new stress level does not exceed the species tolerance limit, species abundance will stabilise at a new (equilibrium) level. This new (equilibrium) level may be the result of e.g. increased mortality of individuals, reduced growth rates, reduced reproduction, etc., in response to e.g. reduced resources or physiological limitations. When the stress level at a specific location exceeds the species tolerance level too long, the species will be eventually lost at such a location. Before this point is reached, however, timely stress remediation may prevent species loss. Where (abundance level) and when (response time) this point is reached is difficult to predict and depends on species' specific resilience. Removing stress not necessarily immediately leads to improvements. A downward trend may continue for some time and could still result in the loss of a species. In general, the closer to its tolerance limits a species persists, the more vulnerable it will be to disturbances.

Combining Graphs

Combining the species response curve shown in Fig 1 (note: we only show one part of the curve between maximum and zero abundance, by plotting stress level from no stress optimal conditions to stress levels beyond a tolerance limit) and the species response trajectory curves shown in Fig. 2, results in a 3D representation of how species respond over time to increased stress levels due to changing environmental parameters from optimal at t=0, to the stress level indicated in the figure (Fig. 3). Making a 2D top-view projection of Fig. 3, results in species abundance iso-lines (in % of t=0 value) from which one can see the resulting abundance (proxy for health status) of a species (colours) as function of stress level and exposure time to that stress level. In case the combination of stress level x exposure time is too high, species cannot persist and will disappear.

The actual shape of the species response trajectory depends on the species-specific capacity to acclimate to the imposed stress and the time needed for such acclimation. In case of seagrasses being exposed to light stress, acclimation might involve an increase in chlorophyll content in their leaves as to increase photosynthetic efficiency in response to light reduction and maintain the abundance (Fig. 5). However, if such acclimation is insufficient, other aspects may be affected, ultimately reducing species abundance. If, when and how different response mechanisms are activated determines the development of species abundance over time. Changes in abundance could be gradual or very sudden (see Fig. 7 below), or occur in steps, whereby an initial increase in abundance is not impossible. All schematised curves in this section are (seagrass) species specific, meaning that predicting a community response requires combining this knowledge for different (seagrass) species or assuming that all species in the community behave roughly the same. The latter might be acceptable in case little information is available on individual species making up the community.

Building with Nature interest

Knowledge about species response time and response trajectory shape in relation to stress level is essential to provide useful information to coastal managers and policy-makers for the assessment of potential damage to ecosystems e.g. dredging operations and coastal infrastructural works and to implement protective measures. Reduced light penetration resulting from poor water quality is among the most significant of impacts threatening seagrass ecosystems worldwide (Waycott et al., 2009). For some activities, such as dredging, protective measures can be put into place to minimise the impact of increased turbidity (suspended sediment) and concurrent light reduction, and manage the consequences for seagrass systems (Erftemeijer and Lewis III, 2007). However, this is often not possible. In those cases, ex-ante knowledge about the resilience boundaries of seagrass ecosystems in relation to the expected environmental impact is crucial in the planning and design phase of the operation, in order to avoid irreversible damage or loss.

Seagrass response to light limitation: state of the art

In Singapore seagrasses are concentrated around the smaller islands to the south, but there are also sites along the shores of Singapore's mainland. Most of Singapore’s seagrass meadows are intertidal. Singapore is aware of the need for seagrass protection, monitoring, management, and restoration. The coastal and marine ecosystems of Singapore are however limited and modified by development and the port industry (which is one of the biggest income-earning businesses in the country).For most seagrass species, threshold levels of light reduction are not known, hampering the ability of coastal resource managers to identify impacts and take appropriate measures (Ralph et al., 2007). Seagrasses have the ability to respond to their highly variable light environment and tolerate periods of reduced light availability, balancing photosynthetic (= light dependent) energy production and energy consumption (respiration).

A sequence of possible responses is given in Fig 5 (Collier et al., 2011). How the combination of a reduction in light intensity and the duration of such light reduction cause such responses and control the specific nature and magnitude of adaptations is still poorly understood. Moreover, the latter may differ considerably depending on species-specific growth and survival strategies and the specific environmental setting where the plants grow. Physiological responses can take place on timescales of hours to days, whereas timescales of morphological responses may take weeks to months before they become visible. Visible responses on community scale may take weeks to up to a year, depending on the species composition of a community. Pioneer species usually show a faster response compared to climax species.

In general, fast growing pioneer species with limited biomass and energy reserves and relatively low respiratory energy demands, typically have lower minimum light requirements compared to slow growing climax species with larger biomass and energy reserves and relatively high respiratory energy demands (ecophysiological response range). Yet, these fast growing pioneer species are more sensitive to light reduction and do not tolerate prolonged periods of low light, while slow growing climax species can tolerate much longer periods of light stress (morphological response range) (Collier et al., 2011). On the other hand, the pioneer species recover much faster from the effects of light reduction when light conditions return to normal, whereas the recovery from loss by climax species usually takes much longer and may not occur at all (meadow response range).

How to Use

The construction and interpretation of species response curves is specialists work. It requires ecological laboratory and field work experience and scientific analytical skills. Even the use of a database of species response curves requires additional site specific monitoring of relevant environmental parameters site specific ecological interpretation. Depending on the quality and accuracy of the predicted environmental impact, and its duration, of infrastructural developments, species response curves can be a very powerful tool in the hands of coastal managers, planners and constructors.

1. Experiments
2. Response Trajectories
3. Iterative process

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1. Experiments

In order to determine the vulnerability of seagrasses and seagrass ecosystems to the effects of increased suspended sediment levels (e.g. light reduction and increased sedimentation) laboratory/mesocosm and field experiments and field monitoring programmes may be set-up. These experiments will give insight into different response mechanisms and associated response timescales in relation to stress intensity and stress duration, and the stress resilience of seagrasses, seagrass communities and ecosystems.

Laboratory and mesocosm experiments

Laboratory and mesocosm experiments are especially useful to determine the physiological and morphological responses of a single species to stress under controlled or semi-controlled circumstances. Herewith, by manipulating the stress intensity and duration, the potential specific tolerance limits of a species to a stress factor and threshold values for lethal effects may be determined. The disadvantage is that the plants are taken from their natural environment and placed in an artificial environment which may in itself be a stressful situation. It is also often unclear how plants respond to this handling and to their new environment and to distinguish the effects thereof from the effects of the stress treatment itself.

Field experiments

Field experiments are especially useful to investigate the response of more than one species simultaneously and in their natural environment. These experiments take account of the natural (competitive) ecosystem interactions between different (seagrass) species and individuals and their environment. The resulting tolerance limits of species to a stress factor and threshold values for lethal effects represent more relevant values than the potential tolerance limits determined in lab experiments. Furthermore, these experiments also give insight in responses to stress on ecosystem and community level. The disadvantage is that variations in environmental conditions (e.g. temperature) can often not be controlled and that changes in ecosystem interactions relevant for the interpretation of the results are difficult to predict and to take into consideration beforehand. Furthermore, differences in specific tolerance limits between species may cause one species to respond negatively to the stress factor, and other species to take advantage of the decline in fitness of the more sensitive species and therefore profit from stress, although this may not be the case in a lab experiment. The presence of the one species, in this example, is the limiting factor for the presence of the other species. It is very difficult, if not impossible, to design control treatments for these kind of interactions in the field. Also, natural variation in the investigated stress factor, e.g. light availability, may be larger than the differences in the experimentally applied treatments.

Monitoring

Monitoring of parameters in the field as an alternative to laboratory and field experiments is especially useful if the response mechanisms of species and ecosystems to stress and their tolerance limits are sufficiently documented and that their effects may be predicted. In general, monitoring of field conditions may provide relevant information on baseline data of potential indicators and timescales and extend of natural variation of these indicators on which to build the design of laboratory and field experiments.

Depending on the species and the stress factor examined, experiments to determine the effects of the stress and tolerance limits may take several months up to years. Especially if the effects of repetitive stress or multiple stress factors are important, and if the recovery potential and duration from sub-lethal effects become critical, long-term experiments are unavoidable. Fig. 6 shows an example of species abundance as a function of equal periods of repetitive stress and non-stress intervals in which the species response to stress is faster than the species recovery response. This leads to a stepwise decline in abundance and an increase of the time needed to fully recover from the effect of stress. This will eventually lead to mortality.

Fig. 6: Example of a stepwise decline of abundance as a result of repetitive stress (blue) and insufficient recovery (green) time intervals. The required time for full recovery increases progressively.

Fig. 7: Two examples of possible abundance decline. Blue line describes a sudden decline

The response of a species to stress is not always visible as a gradual decline in species abundance. Often, the abundance declines very slowly until the moment at which a sudden collapse occurs (Fig. 7). If a sudden collapse occurs it is too late to take protective measures. In these cases it is important to identify and monitor indicator parameters that predict the expected species response and that are measures for the nearness to collapse, and that, once changes in these indicators become visible, preventive measures are applicable.

2. Response Trajectories

Following the conceptual diagram of Figure 5, typical ecological and environmental parameters that could /should be investigated or monitored to determine species response trajectories are:

Ecophysiological

These kind of parameters focus on processes that take place at molecular, cellular or tissue level in the plant. Ecophysiological indicators play a role in metabolic biochemical and biophysical reactions and processes in the plant.

- Photosynthetic parameters (photosynthetic performance and photosynthetic efficiency, Maximum productivity (Pmax), Saturation irradiance (Isat: irradiance at which P = 0.5 Pmax), Compensation irradiance (Ic: irradiance at which production equals respiration), Pmax/Isat (as a measure of photosynthetic efficiency))
- Pigments concentrations (chlorophylls, carotenoids)
- Carbohydrate reserves
- Tissue nutrient concentrations (C, N, P)

In response to e.g. a reduction in light availability, as to balance energy production to energy consumption, a seagrass may lower its maximum productivity, saturation irradiance and compensation irradiance, increase its pigments concentrations, and/or mobilise its carbohydrate reserves. These changes may have consequences for tissue nutrient concentrations as well. Physiological indicators should be monitored on a daily (for molecular and cellular responses: photosynthesis parameters, pigments) to maximum weekly (tissue responses: carbohydrates, nutrients) basis.

Morphological

These kind of parameters focus on changes in the appearance of the seagrasses as an adaptation to environmental stress. Fig 8 shows the morphology of some characteristic seagrass designs. A single seagrass shoot typically sprouts from a vertical stem or (vertical) rhizome and consists of a number of leaves. Roots and rhizomes form the belowground plant parts.

- Above and below ground biomass
- Leaf length and leaf width
- Leaf growth rate
- Leaf turnover
- Number of leaves per shoot
- Number of shoots per unit of rhizome length
- Rhizome diameter
- Rhizome growth rate

In response to e.g. a reduction in light availability, as to balance energy production to energy consumption, a seagrass may lower its energy consuming below ground biomass and/or increase its above ground energy producing biomass. Related to this are changes in tissue specific production, growth and turnover rates. In response to e.g. increased sediment accumulation, the seagrass may increase vertical rhizome or leaf growth as to outgrow sediment accretion rates. The ability of a seagrass to do so depends on light availability and/or carbohydrate reserves. Changes in morphological appearance usually coincide with physiological changes. Morphological parameters should be measured on a weekly basis.

Fig. 8: Seagrass design

Community

These kind of parameters focus on changes in the presence and/or appearance of a seagrass species in a community / ecosystem:

- (Specific) seagrass abundance (seagrass cover, specific shoot density)
- Species composition
- Ecosystem health status (ability to recover from perturbations)

In response to stress, depending on the competitive capacities of one species compared to the other, the species composition of an ecosystem or community may change, leading to changes in the (relative) dominance of one species over the other. Community changes usually also involve morphological and physiological changes of a seagrass. Measuring the ecosystem health status in the field could be done by experimentally disturbing the system (e.g. remove plants from a part of the system) and assess how fast it is able to recover from the disturbance. Community parameters should be monitored on a weekly to monthly basis.

Environmental parameters

These kind of parameters focus on changes in the environmental that may have an effect on seagrass fitness and/or seagrass or community functioning:

- Light availability at photosynthetic surface (leaves) and the water surface
- Water temperature
- Turbidity in relation to light availability (suspended solid concentration, algae)
- Suspended sediment composition
- Sedimentation rate and composition
- Nutrient concentration and composition
- Salinity
- Redox
- Soil Sulphate, Sulphide, Fe^{2+}, Fe^{3+} concentrations
- Soil organic content, microbial activity, organic load

In response to changes in environmental parameters, changes in ecophysiological, morphological and/or community parameters are to be expected. As a result of dredging, the suspended sediment concentration in the water column may increase, lowering light availability and/or increasing the sedimentation rate. It is also possible that nutrient and organic load change, which could lead to increased algae production lowering the light availability for seagrasses, or to changes in biogeochemistry related to toxic soil conditions.

In laboratory and field set-ups it is possible to experiment with light and nutrient availability, organic load and sedimentation rate as to assess species specific and/or community responses, or to assess the effect of different (relevant) combinations of multiple stress factors. For manipulative experiments with temperature and salinity, laboratory / mesocosm set-ups are advisable. Many environmental parameters can be monitored constantly using data loggers.

3. Iterative process

Step 1: Niche width and tolerance limits

The establishment of species response characteristics starts with exploring the species niche width and tolerance limits to an environmental parameter. Ideally these can be derived from ongoing field monitoring efforts, e.g. by surveying seagrasses along a depth gradient, from the intertidal until the maximum depth limit, and record as many as possible physiological, morphological, community and environmental parameters. Alternatively, this could be done through literature review or by designing laboratory / mesocosm studies. Seagrasses should be grown from seeds or transplanted from the field in controlled set-ups under a range of different environmental values until it is clear at which values the seagrasses die and at which values the seagrass abundance stabilises at new equilibriums. Prior to the experiment the plants should be allowed sufficient time to acclimate to the laboratory conditions. This can take up to several months. During the experiment the seagrass abundance should be recorded at regular time intervals as to identify the response times and the shapes of the response trajectories at different environmental parameter values.

Step 2: Indicator parameters for decline

The second step involves exploring suitable physiological and morphological indicator parameters for seagrass decline. This could also be done through literature review or, if no sufficient literature data are available, laboratory / mesocosm studies. In addition to recording abundance described for the experiment under step 1 other parameters (such as mentioned above) could be sampled. Step one and two should reveal the species niche width and a number of relevant physiological and/or morphological parameters that could serve as early warning indicators for seagrass loss.

Step 3: Determine recovery criteria

Once niche width and relevant physiological and/or morphological indicator parameters are known, the third step is to determine the recovery potential and recovery time of the seagrasses from environmental stress by submitting the seagrasses to a range of time trials for different stress levels, followed by a recovery period until the seagrass condition has returned to the starting (t0) values. Seagrass abundance and selected indicatorsshould be recorded at regular time intervals. This experiment could be done in laboratory / mesocosm set-ups or in the field. The advantage of field experiments is that the relevance of the selected indicators could simultaneously be tested for applicability under natural conditions and that also community level indicators may be identified. A disadvantage is possible and sometimes unavoidable environmental and ecological differences between stress period and recovery period, although this also gives valuable information about natural heterogeneity. Step 3) could be extended with repetitive stress and recovery treatments as to establish the impact of repetitive stress on recovery potential. Another possibility is to extend step 3) with multiple stress parameters, e.g. besides testing the effects of light reduction due to increased turbidity on seagrass abundance, the additional effects of increased sedimentation, which often co-occurs with increased turbidity, could also be tested. Step 3) gives threshold values for one or more relevant indicator parameters in relation to stress intensity and species response time and recovery potential.

Step 4: Monitoring

The final step involves monitoring of indicator parameters in relation to marine infrastructure projects.

Step 5: Adaptive Management Strategy

Based on the knowledge of species tolerance limits, species response and recovery time and recovery potential obtained from steps 1-4, an ecological relevant indicator value based adaptive management strategy could be designed for dredging and coastal engineering efforts that may cause seagrass systems to decline. The management strategy may set stress time - intensity thresholds for coastal operations parallel to a real-time indicator monitoring and feedback system for the potentially affected seagrass system. Each operation that is potentially harmful for sensitive coastal ecosystems should have a real-time monitoring and feedback system. Thresholds for stress time – intensity should be verified or investigated for each (new or other) coastal ecosystem.

Note:
The selection of an appropriate indicator parameter is critical and not necessarily the same for different seagrass species (e.g. temperate vs. tropical or climax vs. pioneer species) or for the same species in different environments (e.g. height in the (inter)tidal and coastal zone or in mono vs. multi specific meadows). If the occurrence of a species cannot be considered without its ecological context it may be more relevant to identify an indicator for community responses instead of species responses, in which case laboratory / mesocosm experiments are less suitable than field experiments. In any case, the usability of an indicator should be tested for the targeted species or community in the field in the potentially affected area first, before it can be used. The construction of an indicator database for different species, communities and environmental conditions in relation to different forms and intensities of stress factors may prove very instrumental and could be subject for further efforts within the Building with Nature concept.

Practical Applications

1. Singapore mesocosm experiment
2. Field experiments in Singapore and Indonesia
3. Conclusion: Best practice to set safe site-specific dredging criteria

>> Read more

1. Singapore mesocosm experiment

In Singapore the effects of 65 days light reduction and 30 days of elevated temperature was investigated on the tropical seagrass species Halodule uninervis in an outdoor mesocosm experiment at St Johns Island (Nilmawati, 2012). Physiological and morphological parameters were measured to identify possible (early warning) indicators for seagrass decline in response to light and temperature stress. Three different levels of light (Control: 100% Surface Irradiance (SI), moderate (MS): 60%SI, and high shading (HS) 40% SI) were applied using shading screens from day 0 to day 65 and two different temperatures (29oC (day 0 to 65) and 34oC (day 35 to 65)) were applied using aquarium heaters to examine the impact of light and temperature change on physiological and morphological parameters. The chosen light and temperature levels and candidates for indicators were based on literature and monitoring data. Actual light availability followed the natural variation in light levels. Temperature and light levels were recorded every 30 minutes. It is expected that plants will respond to shading with adaptations that allow balancing photosynthetic energy production to respiratory energy consumption. Increased temperature is expected to cause increased respiratory energy consumption, putting additional stress on balancing the plants’ energy budget.

Fig. 9: Mesocosm experiments setup

The light levels used in the mesocosm experiment were compared with literature values for minimum light requirement for Halodule uninervis in the field. Collier et al. (2012) used three ways to express constants for minimum light requirements for Halodule uninervis, taking adaptations to different location specific light regimes into account. These are i) the mean daily irradiance (Id) reaching a minimum value, ii) the percentages of days that a certain daily irradiance value is reached, and iii) the minimum value of hours per days that saturating light irradiance (Isat) is reached (Hsat). Table 1 shows these minimum light requirement constants and the concurring estimates of light availability in the three mesocosm light treatments, assuming that plants have (physiologically) adapted to their respective light treatments. The comparison suggests that HS light availability is at minimum light requirement for one, and below minimum light requirement for two of the tree indicators. It is expected that (prolonged) HS shading will eventually lead to die-off of this seagrass.

Table 1. The mean daily irradiance (Id), 16-18% daily irradiance, and hours saturating irradiance (Hsat) as values for minimum light requirements for Halodule uninervis from Collier et.al (2012) and the corresponding estimates from a mesocosm study for control (100% Surface Irradiance – SI), MS (60% SI) and HS (40% SI) treatments, respectively. Standard deviation in brackets.

	Collier	Control	MS	HS
Id (mol m-2 d-1)	5	10 (4)	6 (3)	5 (2)
16-18% daily irradiance (mol m2 d-1)	3	5 (1)	3 (0.3)	2 (0.4)

Hset (h)	4	4.5	3.5	3.5

A significant reduction in leaf width, leaf length, shoot density, number of leaves per shoots, rhizome diameter and rhizome length relative to the starting material was found after 65 days in all light treatments, including the control. Leaf growth and above and below ground biomass also changed in all treatments during the course of the experiment. The morphological parameter results, however, did not differentiate the effects of the light and temperature treatments on seagrass development in this experiment.

Chlorophyll a and b increased in response to shading. Chlorophyll fluorescence showed a pattern that is opposite to the natural irradiance level, but was consistently higher at HS compared to MS and control. Higher chlorophyll fluorescence and higher chlorophyll a and b contents at high shading may indicate a physiological compensation strategy to low light availability as to optimise photosynthetic efficiency, pointing to a survival strategy balancing energy production to energy consumption.

Temperature increase (35 to 65 days) showed a decline in photosynthetic efficiency, probably as a result of a higher respiration rate at 34oC compared to 29oC. The level of stress (light reduction and temperature increase) thus induced a physiological change, the first stage in the response sequence.

Lessons Learned Singapore Mesocosm experiments:

- The results indicate that under the environmental conditions of the mesocosm treatments, Halodule uninervis survives for at least 65 days.

- The measured morphological changes were probably the result of transplanting the plants from the field to the mesocosms and handling of the plants during the experiment, rather than the result of light reduction or temperature increase. The morphological parameters in this experiment could not be used as indicators of change in response to the light and temperature treatments.

- It is clear that the experimental set-up itself provoked significant morphological responses, which illustrates the potential drawbacks of mesocosm / laboratory experiments over field experiments.

- The physiological parameters chlorophyll a and b contents and chlorophyll fluorescence did show a difference in response between seagrasses growing under different mesocosm conditions.

- Chlorophyll a and b contents can be used as indicator if the (natural) plants' chlorophyll content is still well below the maximum (or optimum) chlorophyll content. Leaves with a 'low' natural chlorophyll content, which was the case in this experiment, are able to increase light capturing efficiency by increasing the chlorophyll content, while leaves with a 'high' (maximum) natural chlorophyll content will not profit from increasing the chlorophyll content.

- Large fluctuations in chlorophyll fluorescence following the variations in natural light availability makes chlorophyll fluorescence difficult to use as an indicator in the field. Chlorophyll fluorescence is highly variable (i.e. response time is too short) and is therefore not a practical indicator in the field. The assessment of location and species specific minimum light requirement in combination with light measurements in the field may prove to be a useful indicator predicting the development of seagrass abundance.

- It is advised to i) allow seagrasses to fully adapt to the mesocosm environment until a situation is reached where the number seagrass shoots, the number of leaves and the leaf lengths and widths is stable before commencing experiments, ii) to use measuring techniques that do not negatively affect the fitness of the plants and iii) to run the experiment until a new steady state is reached in all treatments (including complete die-off).

2. Field experiments in Singapore and Indonesia

Within the context of the Singapore Delft Water Alliance (SDWA), several studies on long-term shading treatments were made, both on fast-growing pioneer species as well as slow-growing climax species. In addition to applying long-term shading, also the effect of additional disturbances were tested.

Below a brief summary is given of the main conclusions from the research on the sensitivity of seagrass to turbidity; detailed results will be published separately. The preliminary conclusions from the research so far are:

- Long-term monitoring showed that seagrass meadows in turbid environments like Singapore are surviving close to or at the limits of their tolerance to low light. Additional shading from enhanced turbidity will further decreases seagrass health (Yaakub et al. in prep 1).
- Experimental fieldwork showed that it is possible to test the effect of additional shading on seagrass meadows growing in turbid environments, by applying a novel multi layer shading approach (Yaakub et al. in prep 2).
- Experimental fieldwork showed that increasing turbidity with a similar level may have markedly different effects, depending on the initial health status of the seagrass meadow (Yaakub et al. in prep 2).
- Experimental fieldwork showed that additional turbidity-related shading makes seagrasses increasingly sensitive to other kinds of disturbances, and may cause mortality, where this would not have happened in the absence of this extra turbidity-related shading (Yaakub et al. in prep 3).
- Experimental fieldwork shows that recovery following a disturbance is generally faster in pioneer than climax vegetations, irrespective of shading treatment, and that shading does not seem to cause shifts in species composition (Yaakub et al. in prep 4).
- Long-term shading experiments are extremely hard to carry out in the field due to disruptions from monsoons and other natural phenomena, but such experiments are essential in determining the effect of shading on slow-growing species. As long as the shading is not lethal, plants appear able to recover if original light conditions are restored (Yaakub et al. in prep 5), unless other disturbances interact (Yaakub et al. in prep 3 & 4).
- The shape of a disturbance has consequences for the rate of seagrass recovery (Yaakub et al. in prep 6).

Overall, this work emphasizes that response curves to shading should NOT be looked upon as a fixed relationship; the response is strongly related to the existing condition of the meadow and the probability of the co-occurrence of other disturbances. Both aspects (poor initial health & presence of additional disturbances) make seagrass meadows extremely vulnerable to any additional turbidity-related shading.

Lessons learned – field experiments in Singapore and Indonesia:

The studies clearly demonstrate / have taught us:

1. How to set-up long-term shading experiments in highly turbid areas by using a novel multi layer shading approach, and the great value of the results of such experiments
2. The importance of accounting for the pre-conditioning of a seagrass meadow to assess the impact of further reduction of light conditions
3. The importance of studying the effect of shading on the resilience to additional disturbances as can frequently occur in natural seagrass ecosystems, in order to assess the sensitivity of the seagrass ecosystem to further reduction of light conditions

3. Lessons learned – Best practice to set site-specific safe dredging criteria

The mesocosm studies in Singapore and the field studies showed that the response of a seagrass species and of a seagrass meadow to (additional) light reduction as caused by e.g., dredging, is strongly related to i) the level to which seagrasses are adapted to prevailing environmental conditions ii) the existing condition of the meadow prior to dredging and iii) the probability of the co-occurrence of other disturbances. The latter implies that it is difficult to work with general literature based species response curves, as these general data must always be based on the worst case scenario to be safe.

To set realistic turbidity criteria for a dredging operation, the following best practice is recommended:

- Place cheap light loggers near the seagrass meadow to obtain insight in the temporal variability in light availability and/or turbidity events. Especially in places where dredging is regularly re-occurring, it would be highly beneficial to collect long-time light measurements near the seagrass leaves, to be able to select the optimal dredging periods

- To account for the local seagrass health of the meadow that will be impacted by the dredging plume, one needs to set-up on the dredging site a small-scale shading experiment.

- In case the turbidity level that will be generated by the dredging is known, but the impact on the seagrass over time is unknown, the following experiment is advised. The shading should mimic light reduction of 1.25 x foreseen dredging turbidity. To achieve this one could very well use the novel developed multi layer shading approach. Exaggerating the light reduction by 25% provides a safety margin in predicting the dredging impact on the seagrass. Seagrass health should be monitored over time by measuring cover, specific shoot density and species composition. 5 or more replicate shading frames are recommended.
  Alternatively and in addition, one could determine the minimum light requirements of (the most relevant) seagrass species in the ecosystem and compare these with the light availability under the planned dredging conditions. If the light availability is close to or lower than the plants' minimum light requirements, a sequence of stress and recovery trails is advised as to determine the maximum stress exposure time that will still allow for seagrass recovery (e.g. with field experiments as described above). The planning of the dredging operation should stop before the maximum exposure time is reached, taking a realistic safety margin into account.

- In case the turbidity level that is allowed during dredging needs to be established, but the dredging period is known, the following experiment is advised. A range of shading levels should be created by reducing light level at the seagrass bed by 25%, 50% and 75%. To achieve this one could very well use the novel developed multi layer shading approach. The shading period should be 1.25 x the dredging period, to include a 25% safety margin in predicting the dredging impact. Seagrass health should be monitored over time by measuring cover, specific shoot density and species composition. 5 or more replicate shading frames are recommended per light level.

  Alternatively, one could determine the minimum light requirements of (the most relevant) seagrass species in the ecosystem and expose the segrasses for the intended length of the dredging period to light levels below the minimum light requirements and assess the seagrasses' recovery potential and recovery time.

- In case both the turbidity level that is allowed during dredging, and the dredging period needs to be established the same experiment is recommended as described before (i.e., 25%, 50% and 75% light reduction at the seagrass leaves) and to monitor seagrass health for a period that is at least 1.25 x the period that the dredging could take place

  Alternatively a sequence of stress and recovery trails below minimum light requirements is advised as described above. This assumes that if light availability under dredging conditions is above the minimum light requirements (taking a safety margin into account), seagrass will recover given sufficient recovery time is available.

References

>> Read more

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