Seasonality of a short-lived seagrass relative to environmental factors and the development of an adaptable, functional-structural plant model

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Statement of original contribution

The research presented in this thesis is an original contribution to the field of seagrass ecology and simulation modelling of seagrasses.

The estimated percentage contribution of the candidate to both of the research chapters in this thesis is 80-85%. The research and authorship of this thesis was conducted with the valued assistance of my supervisory panel A/Prof. Michael Renton and Dr Marion Cambridge with the oversight of Prof. Gary Kendrick.

Dr Marion Cambridge provided guidance and support throughout conduct of research and reviewed manuscript drafts for Chapter 2 (The influence of environmental factors on Halophila stipulacea growth dynamics and transplantation in Qatar). A/Prof. Michael Renton provided statistical advice regarding Chapter 2, developed and revised the model reported in Chapter 3 (An adaptable, functional-structural plant model for short-lived seagrasses) in collaboration with the candidate and reviewed manuscript drafts for Chapter 3. Both Dr Cambridge and A/Prof. Renton reviewed the complete thesis and provided comment prior to its submission for assessment.
Abstract

The aim of this study was to investigate the relationships between *H. stipulacea* seasonality and environmental variables, to appraise the feasibility of transplantation in the Persian Gulf (Gulf) and to develop a spatially-explicit, functional-structural plant model (FSPM), where the growth rate of simulated seagrass rhizomes is linked with environmental conditions.

Understanding the drivers of seagrass seasonality is critical to informed management of this important marine habitat. In Chapter 2 I demonstrate that *H. stipulacea* was predominantly short-lived and growth was strongly associated with light irradiance, which is highest in spring and summer. Seagrass rhizomes grew rapidly in spring. The burrowing of crabs in summer and the smothering by mobile macroalgal mats in winter had marked influences on seagrass mortality. Despite the marked seasonality of water temperature, it provided only partial explanation for seagrass growth rate and total rhizome length and this warrants further investigation at shorter sampling intervals and in laboratory controlled conditions.

Extensive coastal development in the Persian Gulf includes large-scale land reclamation projects and there have been recent efforts to offset development impacts by transplanting seagrass from the construction footprint into adjacent areas. The outcomes of a trial *H. stipulacea* transplantation project are also reported in Chapter 2. Although transplantation did not have a significant impact on seagrass growth or survival, almost complete senescence occurred in both transplanted and reference seagrass plots by early spring due to natural seasonality. Thus, transplantation of *H. stipulacea* from and into markedly seasonal environments of the Gulf is unlikely to produce persistent meadows and it should not be considered to be an appropriate mechanism for offsetting habitat losses from construction.

Functional-structural plant models use data describing plant function and structure to simulate higher orders of plant growth. They are useful for integrating current understanding, identifying knowledge gaps and can be used to assess the possible outcomes of management strategies, such as transplantation. In Chapter 3 I report the development and validation of the first spatially-explicit FSPM for seagrasses where rhizome growth rate is controlled by environmental conditions. The model predictions matched empirical data well, although there was more variability in the predictions and the model parameterisation of *H. stipulacea* requires further refinement. This model was
designed to be easily adapted for use with other species and environmental conditions and is freely available using open-source software.
Acknowledgements

The research for this thesis was conducted through the School of Plant Biology, The University of Western Australia.

I would like to express my sincere gratitude to all those who helped me in completing this thesis. Special thanks go to A/Prof. Michael Renton for being a great coordinating supervisor and mentor. Michael has always provided the advice to keep the project on track and has been very supportive throughout my period of study. His commitment and coaching were particularly important during modelling and while I learned to use the statistical computing and graphics package “R”. I am also very grateful to Dr Marion Cambridge for her persistence throughout all phases of the project, particularly while I conducted my research, wrangled data and investigated my findings. Her experience and breadth of knowledge has been a greatly appreciated asset. Prof. Gary Kendrick’s support was critical during project commencement. Without Gary’s agreement to take on a student permanently located on the other side of the world from the university campus, this project would never have commenced.

Great thanks to my partner Marcella di Sessa who, throughout this period of study, gave birth to, and is raising our son Pippin. I couldn’t have finished this project without her support and I feel very lucky to have such a committed, capable and talented partner.
General introduction

This study reports the results of an investigation into the growth dynamics and transplantation of the seagrass *Halophila stipulacea* (Forsk.) Aschers in Qatar, Persian Gulf. Data describing how *H. stipulacea* growth dynamics respond to environmental factors was used to parameterise a computer model that simulates the structural growth of seagrass. The model is designed to be easily re-parameterised to simulate the growth dynamics of other seagrass species and locations. It includes a mechanistic link between environmental factors and seagrass growth dynamics which is particularly useful for the study and management of short-lived seagrasses.

**Seagrass ecological function and conservation status**
Seagrasses are a key component of marine food webs that stabilise sediments and sequester vast amounts of carbon due to their high productivity (Orth et al. 1984; Fonseca 1989; Duarte and Cebrian 1996; Fourquean et al. 2012). They provide valuable nutrient-filtering services and they are the primary food of dugong (*Dugong dugon*) and some sea turtles, some of which are threatened with extinction (Lipkin 1979a; Bjorndal 1980; Marsh et al. 1982; Costanza et al. 1997; Fuentes et al. 2006; IUCN 2010). Seagrass meadows are declining worldwide and some seagrass species are themselves threatened with extinction due to anthropogenic impacts such as dredging, land reclamation, recreational boating, commercial fishing, contaminant discharge, algal blooms, invasive species, sea-level rise and poor land management (Fonseca et al. 2004; Connell and Gillanders 2007; Waycott et al. 2009; Sheppard et al. 2010).

*Halophila stipulacea*
*Halophila stipulacea* is a dioecious tropical seagrass with a native range extending north-east from Mozambique to south west India (den Hartog 1977). *Halophila stipulacea* is a genetically diverse species which reproduces by both sexual reproduction and vegetative growth (Procaccini et al. 1999; Malm 2006). It occurs both in pure stands and in mixed meadows and it tolerates a broad range of sediment type, water temperature, salinity and light irradiance, often exhibiting morphological adaptations to local environmental conditions (den Hartog 1977; Lipkin 1979b; Procaccini et al. 1999; Schwarz and Hellblom 2002; Malm 2006). The extensive seagrass meadows of the Gulf consist of *H. stipulacea*, *H. ovalis* (R. Brown) Hooker f. and *Halodule uninervis* (Forsk.
Aschers.) which together support the second largest population of dugong (*Dugong dugon*) in the world (Preen 1995).

*Halophila stipulacea* occurs as an established invasive species in the Mediterranean and Caribbean Seas, where it was likely introduced via the Suez Canal and was predominantly distributed throughout the southern Mediterranean by translocation of vegetative fragments on commercial and recreational marine transport vessels (Lipkin 1975; Willette and Ambrose 2012). In the Mediterranean Sea it is listed in the top 100 worst invasive marine pests (Streftaris and Zenetos 2006) and in the Caribbean Sea, it displaces the native seagrass *Syringodium filiforme* and supports fewer juvenile fish but an equal or greater abundance of different trophic groups compared to *Syringodium filiforme* (Willette and Ambrose 2012).

**The Persian Gulf**
The Persian Gulf (Gulf) is a shallow, epicontinental sea located between latitudes 24°N and 30°N and longitudes 48°E and 57°E. It experiences minimal water exchange with the Indian Ocean and has an average depth of 35 m (Purser and Seibold 1973). It receives negligible freshwater inflow and high solar irradiance resulting in net evaporation (Hunter 1986). These conditions cause persistently high salinity and a substantial seasonal temperature range, particularly in the shallow waters of the western Gulf (Sheppard 1993).

Whilst the seagrass species of the Gulf are common to the Indo-Pacific bioregion, the extreme environmental conditions and broad seasonal variability in the Gulf limit diversity to the most tolerant of species (Sheppard 1993; Sheppard et al. 2010). Of the 24 seagrass species which occur in the Tropical Indo-Pacific bioregion, only 3 species occur in the Gulf, all of which are small, quick growing and sexually fecund (den Hartog 1970; Price and Coles 1992; Short et al. 2007).

By the early 1990s, more than 40% of the coastline of most Gulf states had been modified by human activities, leading to significant losses of biodiversity and productivity (Al-Ghadban and Price 2002). Although seagrasses are recognised as ecologically and economically important, large coastal construction projects continue to be granted approval to damage seagrass habitat. The construction of the New Doha International Airport (NDIA) in Qatar included the excavation and deposition of 65 million m$^3$ of marine sediments onto heterogeneous seagrass, coral, mangrove and supratidal saltmarsh habitat (Ecology & Environment Inc. 2004;
New Doha International Airport 2013). Also in Qatar, the 26 km² New Port Project (NPP) commenced construction in 2011 and included extensive dredging operations in areas previously consisting of seagrass, coral and mangrove habitat. Seagrasses of the Gulf are also threatened by a high density of polluting industrial activities such as the abstraction and processing of oil and gas and rapid expansion of other industrial developments such as mineral processing and desalination for potable water supply.

Drivers of seagrass growth dynamics
Seagrass growth dynamics are driven by environmental variables, predominantly temperature, light irradiance and nutrient availability, although the relationships often involve complex interactions. Seagrass growth generally increases with increases in temperature, light and nutrients to a threshold, beyond which, growth may slow or cease and eventually senesce (Lee et al. 2007). For example, high water temperature inhibits growth of *Syringodium filiforme* Küntzing in Florida (Barber and Behrens 1985) and *Zostera marina* L. in Korea (Lee et al. 2005) and high light irradiance inhibits seed germination and seedling growth in *H. stipulacea* of the northern Red Sea (Malm 2006). Excessive nutrients are a common cause of extensive seagrass decline such as the widespread historical losses in Cockburn Sound, Western Australia, which was caused by industrial discharge of eutrophic effluent (Cambridge and McComb 1984; Orth et al. 2006). Seagrass growth dynamics are also affected by biological influences such as smothering by macroalgae or damage from herbivory or the burrowing activity of marine fauna (Camp et al. 1973; Orth 1975; Suchanek 1983; Harrison 1987; Valentine and Heck 1991; Valentine et al. 1994; Short et al. 1995; Holmquist 1997; Davis et al. 1998; Townsend and Fonseca 1998).

An understanding of the local drivers of seagrass growth dynamics is critical for effective environmental management. No published literature was found which scientifically demonstrated that seagrasses of the Gulf were either short-lived or perennial. Whilst Basson et al. (1977) suggest that the above ground parts of Gulf seagrasses senesce in winter, the authors did not indicate whether the same applies to below-ground plant parts. Also, Price and Coles (1992) did not identify any relationship between seagrass biomass and season in their 20 month study of seagrasses along the entire Gulf coast of Saudi Arabia. Thus, this study aimed to investigate how environmental variables affect *H. stipulacea* growth dynamics over an annual cycle at a site on the east coast of Qatar.
Seagrass transplantation

Given the ecological and economic importance of seagrass, some effort has been made globally to rehabilitate damaged meadows by transplanting vegetative fragments. Seagrass transplantation has been conducted since (Addy 1947) and comprehensive seagrass restoration guidelines were published by Fonseca et al. (1998), contributing to the current status of seagrass transplantation as an established management technique, albeit one with a high inherent risk of failure. The most common causes of project failure are poor selection of a receptor site, poor implementation, bioturbation by marine fauna, acute storm damage, algal smothering and vandalism (Homziak et al. 1982; McLaughlin et al. 1983; West et al. 1990; Fonseca et al. 1998; Meehan and West 2002; Park and Lee 2007; Bastyan and Cambridge 2008).

Seagrass transplantation has recently been a condition of consent stipulated by the Qatari Ministry of Environment to offset the impacts of multiple large coastal construction projects in Qatar, including the Hamad International Airport in Doha and the New Port Project in Al Wakra. There are four fundamental concerns regarding compensatory seagrass transplantation in the Gulf. Firstly, as discussed above, the annual cycles of growth and senescence for Gulf seagrasses are poorly understood. Interannual survival of short-lived seagrasses typically occurs via a large seed bank or by vegetative growth from small patches of persistent individuals while the majority of the meadow completely senesces (McMillan and Soong; Hammerstrom et al. 2006). If the seagrasses of the Gulf are short-lived, most transplanted fragments would be expected to completely senesce within one year, thus providing negligible ecological return for transplantation effort, unless they persist long enough to set seed in the new environment, their primary mechanism of interannual persistence. Second, seagrass distribution is typically limited to nearshore coastal zones which are rapidly being converted into coastal developments, resulting in progressive loss of suitable space for seagrass habitat. Thus, continued development will result in increasing seagrass loss, regardless of whether or not the developments conduct transplantation. Third, seagrasses are spatially dynamic (Duarte et al. 1994; Marbà and Duarte 1998), requiring surrounding bare patches of sediment to grow into as environmental conditions and resources change. Whilst naturally occurring bare patches at the fringes of a seagrass meadow may appear to be suitable receptor sites for transplants, transplanting into these areas leads to increased seagrass density in areas which may then lead to competition with the native meadow during its colonisation phase. Thus, transplantation into bare patches surrounding seagrass meadows is not likely to adequately offset the
environmental impacts of removing the native seagrass meadow. Finally, Fonseca et al. (1998) reported a median of 35% of transplanted seagrass fragments survive to project completion, based on a review of the outcomes of 53 transplantation projects. Thus, it is highly unlikely that compensatory seagrass transplantation will result in like-for-like habitat replacement of damaged meadows.

Consultants’ reports from the commercial seagrass transplantation projects conducted in Qatar are not available for public review. This lack of public access to grey literature is common throughout the Gulf (Sheppard et al. 2010). I wanted to publicly assess the feasibility of *H. stipulacea* transplantation for future reference by proponents, consultants and natural resource managers.

**Modelling seagrass growth**

Computer simulation growth models are a proven tool for assessing and managing seagrasses. Numerical models have been used to understand the function of seagrass meadows and to assess the impact of human interventions (Wetzel and Neckles 1986; Fong et al. 1997; Best et al. 2001; Newell and Koch 2004). Numerical models were improved for some applications by developing spatially-explicit representation of seagrass growth. Spatially-explicit modelling helps users to “observe” developmental progress which may be logistically difficult or temporally impossible to record empirically (Fonseca et al. 2004; Kendrick et al. 2005). Early spatially-explicit simulations of seagrass growth used a cell-in-filling technique whereby occupied and unoccupied cells of an underlying grid were assigned different colours. Range expansion or contraction was represented by a change in the colour of the grid cells and this approach was effectively used to assess recovery times for damaged meadows and for observing the development of slow-growing seagrass reefs spanning 600 years (Fonseca et al. 2004; Kendrick et al. 2005). However, the scale of these simulations was limited to whole plants or meadows and the subsequent development of functional structural plant models (FSPMs) allowed users to simulate growth and senescence at much finer biological levels.

FSPMs help users to understand and assess plant developmental responses to the underlying biological and physical drivers of biomass change (Godin and Sinoquet 2005; Dejong et al. 2011). Users of FSPMs can define rules for multiple levels of biological structure, such as the function and structure of cells, branches or plants, to predict higher level outcomes, such as the development of branches, plants or meadows (Godin and Sinoquet 2005; Hanan and Prusinkiewicz 2008; Dejong et al. 2011).
Because lower-level data is relatively easy to collect, FSPMs can help circumvent some of the logistical difficulties associated with studying permanently submerged seagrasses. FSPMs are also useful for testing our understanding of plant function, that is, if local-level plant functional processes are correctly understood and represented, then the model based on these will produce more global-level predictions which are an adequate match with empirical observations. However, if the simulated global-level results do not match empirical data, then it is clear that the local-level description of plant functional processes requires further investigation (Godin and Sinoquet 2005).

The clonal growth of seagrasses is well suited to functional-structural plant modelling using a simple set of rules describing the function and structure of individual components of the plant, such as the length of rhizome segments (internodes), rhizome and leaf growth rate, branching frequency and branching angle (Sintes et al. 2005, 2006, 2007; Brun et al. 2006). Brun et al. (2006) built a FSPM to investigate the capacity for seagrasses to adapt its morphology in response to local resource availability. Sintes et al. (2007) developed a spatially-explicit FSPM for seagrasses which incorporated rhizome branching, mortality of rhizome apical meristems and internal signalling to represent dominance of some apical meristems over others. (Renton et al. 2011) designed a FSPM for the slow-growing seagrass *Posidonia australis* Hook. *f.* which was parameterised for a specific set of environmental conditions. Because *Posidonia australis* grows slowly, forming fibrous and damage-resistant rhizomes, it does not exhibit rapid growth or senescence responses to short-term changes in environmental conditions and therefore parameterisation for a specific set of environmental conditions was appropriate (Orth 1975; Valentine et al. 1994; Renton et al. 2011). However, at commencement of this study, no spatially-explicit FSPM was suitable for simulating both the growth and senescence cycles of short-lived seagrasses.

The aims of this modelling study were twofold. Firstly, I wanted to expand on current seagrass models by developing a spatially-explicit FSPM for short-lived seagrasses that could be used to assess the outcomes of management interventions and to test the accepted understanding of the environmental drivers of seagrass seasonality in the Gulf. I selected a shallow subtidal population of the seagrass *H. stipulacea* from the western Persian Gulf for model parameterisation and validation. This population exhibits rapid biomass response to the marked seasonal differences in physical and chemical water quality which it experiences and was thus ideal for testing whether our model could successfully integrate data on lower-level growth processes (at the plant component
level) to predict higher-level behaviour (at the level of whole plants). Secondly, I wanted the model to be adaptable for use with a range of species and locations in future, for it to be freely accessible via open-source software and to have a relatively user-friendly interface for model parameterisation. To enhance the adaptability of the model, I also wanted to establish a mechanistic link describing the effect that changes in environmental conditions have on seagrass biomass.

**Thesis outline**

In addition to this introduction, the thesis consists of two chapters which have been prepared in the style of journal articles, followed by a final chapter providing a general conclusion for the entire thesis.

The first paper, ‘The influence of environmental factors on *Halophila stipulacea* growth dynamics and transplantation in Qatar’ reports an empirical investigation of *H. stipulacea* morphology, growth and senescence rates relative to water quality parameters and light irradiance. The investigation aimed to identify whether the *H. stipulacea* population is short-lived and whether growth dynamics are correlated with any of the sampled environmental factors. Also, the paper reports the outcome of a trial seagrass transplantation project, drawing conclusions as to whether transplantation should be considered a feasible management strategy for this species, in this location.

The second paper, titled ‘An adaptable, functional-structural plant model for short-lived seagrasses’ reports the development of a spatially-explicit, FSPM where growth rate is driven by environmental conditions. The model was parameterised for *H. stipulacea* in Sumaisma Bay, Qatar, based on data reported in Chapter 2, but has been specifically designed to be adaptable for use with other species and environmental conditions. The model was developed in the open source statistical computing and graphics package “R” to maximise its accessibility. Model parameterisation data is contained in comma separated values spreadsheets that can be easily edited using standard software, which makes it easier for users who are not familiar with R or computer programming to reparameterise the model for other species and environments.

The concluding chapter of this thesis describes the achievements, limitations and implications of this project.
Literature cited


The influence of environmental factors on *Halophila stipulacea* growth dynamics and transplantation in Qatar

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Abstract
Seagrasses are under threat in the Persian Gulf (Gulf), a marine environment that experiences a range of anthropogenic impacts from rapid urban and industrial development and is naturally stressful, having high salinity and seasonal extremes of temperature and light irradiance. Commercial seagrass transplantation to offset anthropogenic impacts is a common requirement for development consent in Qatar, but there is a paucity of data describing seagrass ecology. Morphology and growth of the seagrass *Halophila stipulacea* were sampled over 11 months and were related to physical and chemical water quality indicators. Growth and senescence occurred concurrently year-round. Growth was highest in spring (up to 9 mg DW apex\(^{-1}\) day\(^{-1}\)) with plastochron intervals as low as 2 days. Rapid senescence occurred in winter and was exacerbated by the smothering effect of decomposing macroalgal mats in late winter to early spring. Bioturbation by blue swimmer crabs (*Portunis pelagicus*, Linnaeus 1758) caused losses of up to 75% in some recently transplanted plots in summer. Growth rates and morphological parameters were strongly positively correlated with light irradiance and pH, but not only weakly correlated with water temperature. Flowers and fruits were observed during project establishment in May-June but not at completion of the project in May the following year. Transplantation did not have a significant effect on growth rate or total rhizome length. The predominantly short-lived growth habit of *H. stipulacea* indicated that transplantation for the purposes of offsetting the impacts of nearshore construction should not be expected to produce persistent meadows.

Key words
*Halophila* / *stipulacea* / seagrass / aquatic vegetation / growth dynamics / transplantation / seasonality / Arabian Gulf / Persian Gulf

Introduction
Seagrasses are marine angiosperms which constitute a critical marine habitat as they are a key component of marine food webs, stabilise sediments, may be highly productive and sequester carbon (Marbà et al.; Orth et al. 1984; Kenworthy et al. 1989; Duarte and Chiscano 1999). Despite the fact that they provide a suite of ecosystems services from which humanity benefits, seagrasses are experiencing global decline due to anthropogenic impacts (Orth et al. 2006).
*Halophila* species often show marked seasonality, growing quickly during optimal conditions and then senescing (Hillman et al. 1995; Kim et al. 2011). Seasonality of growth is usually driven by changes in light, temperature and nutrients (Williams 1984; Hillman et al. 1995; Erftemeijer and Stapel 1999; Lee et al. 2007; Kim et al. 2011). Interannual survival of local populations typically occurs via a large seed bank or by small, persistent plant fragments (McMillan and Soong; Hammerstrom et al. 2006).

*Halophila stipulacea* (Forsk.) Aschers is a small seagrass naturally occurring in the western Indian Ocean from Mozambique to south western India (den Hartog 1970). It is an invasive species in the Mediterranean and Caribbean Seas, suggesting a range of environmental tolerances (Ruiz and Ballantine 2004; Willette and Ambrose 2012).

The Persian Gulf (Gulf) is an epicontinental sea located between 24°N to 30°N and 48°E to 57°E. It experiences minimal water exchange with the Indian Ocean, negligible freshwater input and has extremely high evaporation due to high solar irradiance (Purser and Seibold 1973). Because of these conditions, salinity in the Western Persian Gulf remains above 40 PSU and shallow subtidal areas often experience a seasonal temperature range from 11°C in winter to 37°C in summer, conditions which are tolerated only by three euryhaline and eurythermal seagrass species (Sheppard et al. 1992; Sheppard 1993). In addition to these natural stressors, by the early 1990s more than 40% of the coastline of most Gulf states had been anthropogenically modified, which resulted in significant losses of biodiversity and productivity (Al-Ghadban and Price 2002). With increasing awareness of the importance of seagrass ecosystems and their global decline, there have been efforts to ameliorate environmental impacts by relocating vegetative fragments of seagrass from within the direct impact zone of coastal development sites to receptor sites outside the construction footprint. Seagrass translocation has been a condition of consent for a number of recent, large coastal construction projects in Qatar, despite a limited understanding of the ecology of these seagrass species and the efficacy of their translocation (Price and Coles 1992; Fonseca et al. 1998).

This study aimed to examine the influence of environmental factors (light, temperature, wind speed and direction, salinity and pH) on *H. stipulacea* growth dynamics over an annual cycle. The study also aimed to compare the effect that transplantation had on seagrass growth and total rhizome length so that natural resource managers have a case study to refer to when considering the feasibility of transplantation for offsetting the impacts of future development applications.
Materials and methods
The study was conducted in the subtidal seagrass meadow of Sumaisma Bay, Qatar (25°55’ N, 51°29’ E) (Figure 1) with a mean water depth of ~0.2 m below chart datum. The patchy meadow consisted of *H. stipulacea*, *Halodule uninervis* (Forsk. Aschers.) and *Halophila ovalis* (R. Brown Hooker f.) and was thus generally representative of shallow seagrass meadows from the Western Persian Gulf (Price and Coles 1992; Sheppard et al. 1992). Whilst assessment of all three seagrass species would have been ideal, the investigation was confined to *Halophila stipulacea* because the density of *Halophila ovalis* was too low to derive meaningful results. The third species, *Halodule uninervis*, has both horizontal and vertical stem growth, introducing a degree of complexity that could not be included in either field measurements or the growth model.

Experimental Design
On 26 June 2011, forty plots of *H. stipulacea*, each measuring 300 mm (length) x 300 mm (width) (an area of 0.09 m²) x 150 mm deep were haphazardly selected from the Sumaisma Bay meadow. Thirty of these plots were to be used for progressive destructive biomass data collection throughout the study period while the remaining ten plots were to be sampled non-destructively. Each transplant plot was manually excavated using a wide-mouth shovel. An open topped aluminium tray was placed over each excavated plot to protect the edges from erosion during underwater transport to the
receptor site, which was located within a 15 m radius from the donor site. The transplant plot was buried flush with the level of the seabed at the receptor site. Any gaps between the transplant and the surrounding sediment were filled in using surplus soil. Each transplanted plot contained 1-4 separate lengths of rhizome, each with between one and six apical meristems. *Any Halodule uninervis or H. ovalis* plants within the translocated plot were gently removed and discarded. 10 additional plots were selected from the margins of the surrounding meadow and established as reference plots. A further 10 0.09 m² plots were transplanted on 5 April 2012 for the purpose of collecting detailed spring growth data (Table 1). A 300 mm length of reinforcing steel was driven into the seabed at the southwest corner of each plot and a Coburn© cattle ear tag with unique identification number was attached to each stake using a plastic cable tie.

Table 1: Summary of the experimental design. Unless stated otherwise, sampling was conducted on 26 June 2011, 26 August 2011, 21 October 2011, 7 January 2012, 23 March 2012, 5 May 2012 and 21 May 2012.

<table>
<thead>
<tr>
<th>Experimental component</th>
<th>Sampling method</th>
<th>Number of sites/samples</th>
<th>Sampling frequency/dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environmental sampling</td>
<td>In-situ physical and chemical water quality</td>
<td>1 site</td>
<td>~2 monthly</td>
</tr>
<tr>
<td></td>
<td>Sediment for total organic carbon and particle size analysis</td>
<td>1 consolidated sample</td>
<td>5 April 2012</td>
</tr>
<tr>
<td></td>
<td>Deployed light and temperature logger</td>
<td>1 site</td>
<td>Continuous at 15 minute intervals</td>
</tr>
<tr>
<td>Reference seagrass</td>
<td>Non-destructive anatomical measurement</td>
<td>10 seagrass plots</td>
<td>~2 monthly</td>
</tr>
<tr>
<td>Transplanted seagrass</td>
<td>Destructive biomass sampling</td>
<td>30 seagrass plots (5 plots destructively sampled on 6 events)</td>
<td>~2 monthly</td>
</tr>
<tr>
<td></td>
<td>Non-destructive anatomical measurement of seagrass sampled for annual growth variation</td>
<td>10 seagrass plots</td>
<td>~2 monthly</td>
</tr>
<tr>
<td></td>
<td>Non-destructive anatomical measurement of plots sampled for spring growth rate</td>
<td>10 seagrass plots</td>
<td>5 April 2012, 20 April 2012, 21 May 2012</td>
</tr>
</tbody>
</table>

Salinity, pH and turbidity were sampled at ~2 month intervals using a calibrated YSI 6000© water quality sampler. Temperature and light were recorded at 15 minute
intervals with a HOBOware temperature and light logger (product number UA-002-64) installed 100 mm above the seabed at the receptor site and periodically downloaded in-situ. Any material which had fouled the light sensor, such as sediment or algae, was wiped off prior to download. Only light data recorded within five days of cleaning the sensor was used for analysis to reduce the influence of biofouling and silt deposition which rapidly accumulated. Daily wind speed and direction data were obtained from the Doha International Airport (http://www.weatherspark.com).

Two composite sediment samples were collected on 10 February 2012 from the top 100 mm of the seabed throughout the study site by laying an open, plastic sample bag on the seabed and pushing sediment into the bags using a stainless steel diver’s knife. Total organic carbon (TOC) was analysed by acid digestion then dry weighed and dry combusted with a LECO CR-412. Briefly, residual carbon dioxide gas passes through a non-dispersive infrared detector, and the mass of carbon present is recorded and then converted to a percentage of the dry sample weight. Grain size distribution was determined by sieve analysis (British Standard 1377 1990). Samples were dried in an oven at 70 - 80°C for 24 hours and then sieved in a standard sieve stack into seven size classifications: >2 mm (granule), <2 mm to >0.063 mm (sand) and <0.063 mm (fines) (Endecotts Ltd). Each sample was shaken by automatic shaker for 15 minutes, the size fractions weighed and their proportions then calculated (Inman 1952; Gray 1981).

Plant parts were measured in situ at ~2 month intervals. The overlying surface layer of fine sediment was gently fanned away to expose the seagrass rhizomes (Hillman et al. 1995). As the rhizome’s apical meristem grows it produces a pair of leaves each encased in a leaf sheath which encircles the rhizome. As the leaf sheaths senesce they leave a scar on the rhizome and the portion of rhizome between scars is called an internode. The length of rhizome internodes, branch location, branch angle from the main stem, presence or absence of leaves, length of leaves and location of apical meristems were recorded in each plot using a flexible plastic ruler and protractor where relevant. The number of internodes between branches was recorded from the first branch to subsequent branches and the presence or absence of a root was noted. All data were recorded on DuraRite© underwater paper using a graphite pencil. The number of apical meristems and leaf pairs within each 0.09 m² quadrat was divided by 0.09 to derive values for shoot density m⁻² for comparing data with results in published literature.
An initial attempt to track rhizome growth and senescence rates was conducted by tagging rhizomes using plastic-coated metal pegs which were driven into the seabed at rhizome branches and apical meristems. Seagrass which had grown beyond the pegs was identified as new growth. This method was successful for short-term sampling trials, however, because sampling intervals for the main study were generally long (~2 months) and plant turnover was rapid, this method was impractical as were other rhizome or leaf tagging methods reported in the literature. Therefore, growth and senescence rates were calculated for each plot using the detailed record of the number of internodes present. The change in the total number of internodes between subsequent sampling events was divided by the number of apices present at the commencement of the sampling period and the number of days in that sampling period to calculate plastochron interval (Patriquin 1973). Growth and senescence rate (mm apex⁻¹ day⁻¹) was calculated in a similar manner by dividing the change in total rhizome length by the number of apices and days in the sampling period.

At each sampling event, five of the 30 transplanted plots designated for biomass data collection were randomly selected and excavated. Sediment was removed from the samples prior to placing them in a Ziploc© bag with identification number and seawater which was chilled then transported immediately to the laboratory. Epiphytic sediment and algae were washed or gently rubbed off the plants and the number and length of internodes, leaves and roots were recorded. Samples were separated into plant-part groups of rhizome, leaf or root for each plot. Samples were dried at 60°C to a constant weight which was measured using a Shimadzu Corp AY220 analytical balance.

Dry weight data for each plant-part group were divided by the number of internodes, leaves and roots sampled to derive mean mass for each individual plant-part. The mean mass of each individual plant-part was summed to derive the mean mass of a single module which consists of a single internode with leaf pair, leaf sheaths and root. Overall biomass (mg DW m⁻²) was calculated by multiplying the recorded leaf pair density in each plot by the mean mass of a module. Total dry weight for each plant-part group was divided by the total length of each corresponding plant-part group to derive values for calculating biomass production and senescence rates (mg DW mm⁻¹). The ratio of above- to below-ground plant-parts was calculated by dividing the total mass of leaves with leaf sheaths by the sum of the mass of rhizomes and roots. Biomass accumulation rate (mg DW apex⁻¹ day⁻¹) was calculated by dividing the mass of a single module by the plastochron interval. Biomass accumulation rates were then multiplied by apical
density to convert values to biomass accumulation rate per unit area (mg DW m\(^{-2}\) day\(^{-1}\)) for comparison with published literature.

**Statistical treatment**

Data were analysed using the open-source statistical computing and graphics package ‘R’ (R Core Team 2013). Welch’s t-test was used to test for differences between reference and transplanted seagrass for growth rate (mm apex\(^{-1}\) day\(^{-1}\)) and the total length of seagrass rhizome. Multiple linear regression was conducted using the Akaike information criterion (AIC) method (Akaike 1974) to test whether growth variables were affected by explanatory environmental variables (Crawley 2007). Explanatory environmental variables used were temperature, relative light irradiance, wind, salinity and pH. Light, temperature and wind data were sourced from continuously logged data and the mean value for the three weeks immediately preceding each sampling event was used in conducting multiple linear regression.

**Results**

**Physical and chemical environmental factors**

Table 2 shows water temperature on the day and time of the six sampling events. The full range of water temperatures (not shown) were logged at 30 minute intervals over the full year of the study and ranged from 7 °C in winter to 40 °C in summer. Light levels ranged from 4127 lux in winter to 9062 lux in summer (Table 2). Salinity was less seasonal, mostly in the mesohaline range (43-46 RSU) but with lower values recorded on 7 January (40 RSU, winter). The strongest winds were predominantly north-westerly and gusts frequently exceeded 15 m s\(^{-1}\) (~40 km h\(^{-1}\)) from January to March 2012. These periods of strong winds fragmented and dislodged seagrass rhizomes, increased turbidity due to wave-stirring in the shallow sub-littoral site, deposited desert dust into the water and in winter moved detached macroalgal mats across the seafloor.

Sediments were predominantly silty sands, consisting of 81% sand fractions, 9% fines and 10% granules with 2.7% organic matter.
Table 2: Summary of water quality and biomass data collected on each sampling event. ‘ND’ denotes that no data were collected.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Temp (°C)</th>
<th>Salinity (RSU)</th>
<th>Light (lux)</th>
<th>pH</th>
<th>Mean wind speed (m s⁻¹)</th>
<th>Turbidity (NTU)</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 June 2011</td>
<td>32</td>
<td>44.1</td>
<td>9062</td>
<td>8.1</td>
<td>4.3</td>
<td>15.2</td>
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<tr>
<td>26 August 2011</td>
<td>33</td>
<td>43.5</td>
<td>3728</td>
<td>7.6</td>
<td>3.8</td>
<td>5.7</td>
</tr>
<tr>
<td>21 October 2011</td>
<td>31</td>
<td>43.1</td>
<td>4628</td>
<td>7.9</td>
<td>3.8</td>
<td>4.1</td>
</tr>
<tr>
<td>7 January 2012</td>
<td>24</td>
<td>40.4</td>
<td>4127</td>
<td>8.0</td>
<td>3.4</td>
<td>10.6</td>
</tr>
<tr>
<td>23 March 2012</td>
<td>20</td>
<td>45.3</td>
<td>6869</td>
<td>8.1</td>
<td>5.2</td>
<td>41.7</td>
</tr>
<tr>
<td>5 April 2012</td>
<td>24</td>
<td>45.3</td>
<td>6284</td>
<td>8.1</td>
<td>4.8</td>
<td>41.3</td>
</tr>
<tr>
<td>20 April 2012</td>
<td>26</td>
<td>44.7</td>
<td>7011</td>
<td>8.1</td>
<td>3.7</td>
<td>5.32</td>
</tr>
<tr>
<td>5 May 2012</td>
<td>26</td>
<td>46.6</td>
<td>7324</td>
<td>8.3</td>
<td>3.3</td>
<td>3.21</td>
</tr>
<tr>
<td>21 May 2012</td>
<td>32</td>
<td>ND</td>
<td>7578</td>
<td>ND</td>
<td>3.4</td>
<td>ND</td>
</tr>
</tbody>
</table>
Growth rate and biological interactions

Rhizome growth rate (mm apex\(^{-1}\) day\(^{-1}\)) was variable but the overall seasonal trend was one of growth in spring followed by senescence in autumn and winter. The growth rate of transplants was highest in May 2012 (spring) but some reference plots were smothered by decaying macroalgae in May 2012 causing the continued decline observed until the project ceased (Figure 2). Plastochron intervals were shortest on 26 August 2011 and 21 May 2012 (~2 days) and the quickest internode senescence rate was also recorded on 21 May 2012 (also ~2 days) (Table 3). The horizontal growth of apical meristems across the seabed occurred concurrently with senescence of the oldest internodes. This senescence pattern resulted in separation of branches from their parent stems. Rapid senescence occurred in early spring due to smothering by decaying macroalgae which settled in mats up to 50 mm thick on the seabed (Figure 4). Smothering by macroalgae caused extensive senescence in reference plot 40, leading to the observed decline in total rhizome length and growth rate in reference plots compared with transplants (Figure 2, Figure 3).

Biomass accumulation rate (mg apex\(^{-1}\) day\(^{-1}\)) and the biomass of individual modules and whole plants was highest in August 2011 (Table 3). Biomass accumulation rate (mg apex\(^{-1}\) day\(^{-1}\)) was lowest on 23 March and 5 May 2012 and a corresponding seasonal trend was recorded for leaf pair density and apical meristem density with the highest values recorded in August 2011 and the lowest values on 5 May 2012 (Table 3). There was no significant difference between transplants or reference plots for either growth rate (mm apex\(^{-1}\) day\(^{-1}\)) (t = -0.39, p = 0.70) or total rhizome length (t = -0.67, p = 0.51).

Flowers and fruits were recorded in May and June 2011 but not again until project completion on 21 May 2012. Dense, mobile mats of macroalgae were not present in May 2011 but were observed from March 2012 until project completion in May 2012.

Blue swimmer crabs were observed when water temperature consistently exceeded ~28 °C. By burrowing in the sediment, with a preference for the loose sediment at the margins of transplanted seagrass plots, they caused losses of up to 75% of the seagrass in some plots, although their impact on the wider, established meadow was much lower. Dense, mobile mats of macroalgae were found entangled in the label identification stakes on 23 March, 5 May and 21 May 2012 and their decay caused rapid senescence in smothered plots.
Table 3: Leaf pair density, apical density, maximum plastochron interval (PI), maximum internode senescence interval (ISI), biomass of a leaf pair with a single rhizome and root of mean length (module biomass), biomass, ratio of above to below ground biomass (A:B), and biomass accumulation rate (BAR) for each sampling event. n: number of samples. ND: no data. Leaf pair density and apical density: mean (standard error). *: values calculated using mean module mass from August 2011, October 2011 and January 2012 data with reference and transplant data pooled (distinction is provided in subsequent figures). #: 2011 reference and transplant data. ^: spring 2012 transplant data. Ref=reference, Tran=transplants, Spring tran=spring transplants.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Leaf pairs/ m²</th>
<th>Apex/ m²</th>
<th>PI (day)</th>
<th>ISI (day)</th>
<th>Module biomass (mg DW)</th>
<th>Biomass (g DW m⁻²)</th>
<th>A:B Biomass ratio (n=5)</th>
<th>BAR (g DW m⁻² day⁻¹)</th>
<th>% of sampled plots with live plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>26-Jun-11 n=50</td>
<td>161</td>
<td>54</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>Ref: 100</td>
</tr>
<tr>
<td>26-Aug-11 n=9</td>
<td>440</td>
<td>111</td>
<td>2</td>
<td>51</td>
<td>18.4</td>
<td>13.5</td>
<td>1.51</td>
<td>1.02</td>
<td>Ref: 100</td>
</tr>
<tr>
<td>21-Oct-11 n=25</td>
<td>100</td>
<td>53</td>
<td>6</td>
<td>20</td>
<td>5.8</td>
<td>1.1</td>
<td>0.79</td>
<td>0.05</td>
<td>Ref: 90</td>
</tr>
<tr>
<td>7-Jan-12 n=40</td>
<td>88</td>
<td>32</td>
<td>6</td>
<td>9</td>
<td>3.8</td>
<td>0.6</td>
<td>1.26</td>
<td>0.02</td>
<td>Ref: 66</td>
</tr>
<tr>
<td>23-Mar-12 n=35</td>
<td>15 (2.6)</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>0.01*</td>
<td>Ref: 30</td>
</tr>
<tr>
<td>5-Apr-12 n=10</td>
<td>210</td>
<td>50</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>Ref: NA</td>
</tr>
<tr>
<td>20-Apr-12 n=10</td>
<td>181</td>
<td>59</td>
<td>6</td>
<td>10</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>0.09*</td>
<td>Ref: NA</td>
</tr>
<tr>
<td>5-May-12 n=30</td>
<td>13 (2.6)</td>
<td>7 (1)</td>
<td>9</td>
<td>6</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>0.01*</td>
<td>Ref: 30</td>
</tr>
<tr>
<td>21-May-12 n=35</td>
<td>97 (16.3)</td>
<td>27 (5)</td>
<td>2</td>
<td>2</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>0.15*</td>
<td>Ref: 20</td>
</tr>
</tbody>
</table>

Note: Spring tran: NA
Figure 2: Growth rates of *Halophila stipulacea* (coloured symbols and lines) compared to mean monthly water temperatures derived from data collected by continuous loggers (vertical grey bars), Sumaisma Bay, Qatar. Growth rates measured as the change in the number of internodes apex$^{-1}$ day$^{-1}$.
Figure 3: Mean rhizome length of *Halophila stipulacea* (coloured symbols and lines) compared to mean monthly water temperatures derived from continuous logger data (vertical grey bars), Sumaisma Bay, Qatar.
Relationships between environmental factors and growth

Growth rate (mm apex⁻¹ day⁻¹) was strongly correlated with light and pH but the correlation with daily mean water temperature was only slightly significant or not at all significant under two different models with equally good (low) Akaike Information Criterion (AIC) values (Table 4). Longer rhizome segments were associated with higher light, temperature and pH while total rhizome length was greater with higher light and pH (Table 4).

Results summary

In summary, the H. stipulacea population in Sumaisma Bay is largely short lived and although a small number of individuals survived through winter, the general trend was of rapid rhizomatous growth in spring with rapid senescence in autumn and winter. A new leaf pair was formed in as little as <2 days and rhizomes spread across the seabed at rates of up to 2.1 mm apex⁻¹ day⁻¹.
Table 4: Results of multiple linear regression testing of the effects of environmental variables on aspects of plant morphology with f-value in brackets. ***: p<0.001, **: p<0.01, *: p<0.05, ns: not significant. AIC values represent the fitted model coefficients.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Temp</th>
<th>Light</th>
<th>Wind</th>
<th>Salinity</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth rate model 2 (AIC = -251.8)</td>
<td>*(4.2)</td>
<td>**(10.1)</td>
<td>ns</td>
<td>ns</td>
<td>*** (18.0)</td>
</tr>
<tr>
<td>Growth rate model 2 (AIC = -251.8)</td>
<td>ns</td>
<td>*(5.5)</td>
<td>ns</td>
<td>ns</td>
<td>*** (15.9)</td>
</tr>
<tr>
<td>Total rhizome length</td>
<td>ns</td>
<td>***(14.4)</td>
<td>*(4.5)</td>
<td>ns</td>
<td>*** (22.2)</td>
</tr>
<tr>
<td>Internode length</td>
<td>ns</td>
<td>***(37.3)</td>
<td>ns</td>
<td>** (10.2)</td>
<td>ns</td>
</tr>
<tr>
<td>Internode angle</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>** (9.1)</td>
<td>ns</td>
</tr>
<tr>
<td>Rhizome segment length</td>
<td>*(5.5)</td>
<td>***(30.1)</td>
<td>ns</td>
<td>ns</td>
<td>*** (20.2)</td>
</tr>
<tr>
<td>Number of internodes per segment</td>
<td>****(16.6)</td>
<td>***(37.2)</td>
<td>**(7.0)</td>
<td>ns</td>
<td>***(30.4)</td>
</tr>
<tr>
<td>Branching frequency</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Ratio of internodes with versus without leaves</td>
<td>****(21.9)</td>
<td>***(62.1)</td>
<td>***(27.8)</td>
<td>*(4.7)</td>
<td>***(57.4)</td>
</tr>
</tbody>
</table>

Discussion

The marked seasonality observed in this study is typical for small, quick-growing seagrasses, particularly those which occur in locations with broad seasonal differences in environmental conditions, such as the Gulf (Dunton 1994; Hillman et al. 1995; Kenworthy 2000; Lee et al. 2006; Kendrick et al. 2008). Those few individuals which persisted through the winter senescence period may be genetically adapted to overwinter, as *H. stipulacea* is genetically diverse (Procaccini et al. 1999) but it is apparent that the population is generally short-lived. The marked seasonality observed in this study does not support the results of Price and Coles (1992), who did not identify any correlation between seagrass biomass and season in their 20 month study of seagrasses at eight sites on the Saudi Arabian Gulf coast. Seagrass meadows are spatially dynamic and in Qatar, the three quick growing seagrasses often occur in patches of variable shoot density which may be interspersed with corals, macroalgal beds and bare sand. This dynamic and heterogeneous distribution emphasises the
importance of fixed quadrats when conducting repeat surveys and may partially explain the lack of seagrass seasonality reported by Price and Coles (1992). Also, given that deeper waters are less influenced by atmospheric temperature variability, it is possible that seasonality is less apparent in meadows occurring the deeper waters, such as some sites sampled by Price and Coles (1992).

Seagrass seasonality is commonly associated with light irradiance, temperature and nutrient availability (Park and Lee 2007) but in this study, indicators of seagrass growth were most strongly correlated with light irradiance and pH. The shallow sublittoral study site was characterised by marked seasonal variability in light irradiance and water temperature, persistent high salinity >40 PSU and a pH range of 7.6 to 8.3. The range in environmental data is consistent with other published literature which identifies the Gulf as an extremely stressful marine environment (Price and Coles 1992; Erftemeijer and Shuail 2012; Quigg et al. 2013). The weaker relationship with temperature is surprising, as it is often cited as a key influence on growth. The optimal temperature for tropical seagrasses of 32°C as proposed by (Lee et al. 2007) was consistently exceeded throughout summer and although the 24-hour mean temperature remained below the upper tolerance threshold of 37°C proposed for seagrasses of the Gulf (Erftemeijer and Shuail 2012), water temperature was often sustained above 37°C throughout summer days. High summer temperatures did not clearly cause senescence, as may be expected due to thermal inhibition but highest growth rates actually coincided with highest water temperature while marked senescence coincided with declining temperatures through autumn. However, the time-lag owing to the two-monthly sampling interval may have masked seagrass responses to environmental conditions, particularly for the short period of water temperature that exceeded 37°C between mid-July and early-August. Thus, further detailed assessment of growth parameters and temperature such as may be derived from conducting studies as short intervals of around 2 weeks or by conducting laboratory experiments is warranted and may identify that temperature has a more significant influence than the findings reported here (Barber and Behrens 1985; Bulthuis 1987; Lee et al. 1996, 2007; Campbell et al. 2006). The strong relationship between growth parameters and pH may be an artefact of the particularly low pH data obtained on 26 August 2011 that coincided with marked senescence. Ambient air temperature at the study site in mid-summer persistently exceed 40°C which may have hastened deterioration of the pH probe resulting in the subsequent low pH data obtained on 26 August 2011 (7.6 pH units).
Maximum biomass accumulation rates per rhizome apex, up to 9 mg DW apex\textsuperscript{-1} day\textsuperscript{-1}, is substantial compared with Halophila populations recorded elsewhere but productivity per unit area is lower, in part due to the sparse distribution of seagrasses sampled in this study (Table 5). Productivity data for this study was derived from seagrasses growing at the fringes of existing meadows (reference) or in isolated fragments (transplants). Sparsely distributed seagrasses typically exhibit more rapid growth and rhizome extension than those growing in the centre of a densely packed stand (Gallegos et al. 1993; Vidondo et al. 1997; Marbà and Duarte 1998). Also, removal of Halodule uninervis and H. ovalis at the commencement of the study may have increased the growth rate of the H. stipulacea individuals studied due to reduced competition. Thus, the values provided here are considered to adequately represent the high end of the productivity range and may be lower in denser stands.

Total plant biomass was low in this study (0 - 13.5 g DW m\textsuperscript{-2}) compared to records from other locations. Even off Mesaieed in south-eastern Qatar, Delft Hydraulics (2005) reported higher total plant biomass of \( \sim 37 \) g DW m\textsuperscript{-2} in H. stipulacea dominated meadows (Table 5). Sparsely populated seagrass plots were preferentially selected for this study so that each sampling event could be completed within two consecutive days to reduce potential within-sample variability which may otherwise result from extended sampling periods. Thus, the biomass values reported here are not representative of biomass within the broader seagrass meadows, which can be substantial. Despite the small size of the three seagrasses which occur in the Gulf, seagrass meadows cover an area of \( \sim 7,000 \) km\textsuperscript{2} and their collective biomass supports the second largest population of Dugong (Dugong dugon) in the world (Sheppard 1993; Preen 1995; Sheppard et al. 2010; Erftemeijer and Shuail 2012).

The decomposing macroalgal masses observed accumulating over stands of seagrass in winter and early spring clearly had a deleterious effect on the productivity of H. stipulacea. This is likely to be the result of both direct shading of the leaf canopy as well as altering gas exchange at the water column: sediment interface. These conditions increase the likelihood of hydrogen sulfide intrusion into seagrass tissues (Koch 1994; Holmer and Nielsen 2007; Cambridge et al. 2012), as well as increasing boundary layer thickness at the leaf surface, which reduces the availability of carbon for photosynthesis (Larkum et al. 2003). H\textsubscript{2}S is a potent phytotoxin which has been implicated in broad scale senescence of seagrass meadows, although recent studies suggest that it is a synergistic factor that predominantly adversely affects seagrasses during periods of high

The natural complete senescence of most *H. stipulacea* individuals sampled in this study is pertinent to the commercial seagrass transplantation projects regularly conducted throughout Qatar and the Gulf. Almost complete natural senescence occurred by early spring regardless of whether seagrasses in this study were previously transplanted. If the goal of a transplantation project is to offset the environmental impact of displacing seagrass habitat by moving it elsewhere, the outcomes of transplantation are likely to be at worst, complete failure due to senescence and at best, far less than like-for-like replacement. Thus, transplantation for the purposes of offsetting the direct environmental impact of displacement due to land reclamation is unlikely to adequately satisfy this goal. Interannual persistence of the population is likely heavily dependent on sexual reproduction by seed (Kenworthy 2000; Rasheed 2004). Seed-based colonisation has been reported for another small, quick growing Gulf seagrass species, *Halodule uninervis* which has spontaneously colonised physically suitable areas created by some recent, large-scale coastal developments in the Gulf (Josselyn et al. 1986; Kenworthy 2000; Erftemeijer and Shuai 2012). Rather than transplanting seagrasses for the purpose of offsetting environmental impacts, greater ecological benefit would be achieved by impact avoidance or by appropriately designing coastal construction projects to facilitate natural recolonisation. The rapid rate of coastal development in the Gulf seems likely to continue to have negative implications for the productivity, species diversity and population density of the Gulf’s marine organisms unless more appropriate and informed approaches to environmental management are adopted (Sheppard et al. 2010).

This study has demonstrated that *H. stipulacea* in Sumaisma Bay is principally short-lived, that it is seasonally highly productive and that growth is primarily associated with light irradiance. It is an important step toward understanding a marine environment that is experiencing rapid development and a range of anthropogenic impacts and it clarifies some misunderstandings in the published literature which have not identified seagrass seasonality in the western Gulf (Price and Coles 1992). Scientific understanding of the influence of environmental parameters on seagrass seasonality in the Gulf would benefit from further detailed investigations combining field and laboratory experiments and investigation of the growth dynamics of other seagrass species which comprise the Gulf community; *H. ovalis* (R. Brown Hooker f.) and *Halodule uninervis* (Forsk.) Aschers.
Table 5: Comparison of growth parameters for *H. stipulacea* in this study with *Halophila* species in the literature

<table>
<thead>
<tr>
<th>Source</th>
<th>Species</th>
<th>Location</th>
<th>Water Depth (m)</th>
<th>Apical Density (m⁻²)</th>
<th>Biomass (g DW m⁻²)</th>
<th>Production (g DW m⁻² day⁻¹)</th>
<th>Net Production (mg DW apex⁻¹ day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>This study</td>
<td><em>H. stipulacea</em></td>
<td>Qatar (turbid water)</td>
<td>0.2</td>
<td>7-111</td>
<td>0.6-13.5</td>
<td>0 – 1</td>
<td>0 – 9</td>
</tr>
<tr>
<td>Wahbeh 1984ᵃ</td>
<td><em>H. stipulacea</em></td>
<td>Aqaba, Jordan</td>
<td>10</td>
<td>403.5</td>
<td>ND</td>
<td>2.2</td>
<td>4.5</td>
</tr>
<tr>
<td>Kenworthy et al. 1989</td>
<td><em>H. decipiens</em></td>
<td>US Virgin Is.</td>
<td>15</td>
<td>3900</td>
<td>20.1</td>
<td>2.9</td>
<td>0.7</td>
</tr>
<tr>
<td>Erfetmeijer and Stapel 1999ᵇ</td>
<td><em>H. ovalis</em></td>
<td>Indonesia</td>
<td>12-16</td>
<td>373</td>
<td>24</td>
<td>2.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>5.2</td>
</tr>
<tr>
<td>Hillman et al 1995</td>
<td><em>H. ovalis</em></td>
<td>Western Australia (turbid water)</td>
<td>1-2</td>
<td>~100-1300</td>
<td>80-100</td>
<td>1.5</td>
<td>&lt;2.1&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Where:

ND - no data

ᵃ Data for above ground plant parts only

ᵇ Data converted by dividing ash free dry weight by 0.45 to derive dry weight (Erfetmeijer and Stapel 1999)

ᶜ Calculated with the formula: mean plant unit mass / mean plastochron interval x apical meristem density

ᵈ Laboratory trial data
Literature cited


Hammerstrom KK, Kenworthy WJ, Fonseca MS, Whitfield PE. 2006. Seed bank, biomass, and productivity of Halophila decipiens, a deep water seagrass on the west Florida continental shelf. Aquatic Botany, 84: 110-120.


An adaptable, functional-structural plant model for short-lived seagrasses

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Abstract

Background and Aims Short-lived seagrasses are important marine habitats which respond rapidly to environmental changes but are logistically difficult and expensive to study. A model that simulates the growth and senescence of short-lived seagrasses relative to environmental influences was developed to integrate our understanding of seagrass growth dynamics and to assess options for potential management interventions, such as seagrass transplantation.

Methods A functional-structural plant model was developed where growth and senescence rates are mechanistically linked to environmental parameters. The model was parameterised and validated for a population of *Halophila stipulacea* in the Persian Gulf.

Key Results There was a good match between empirical and simulated results for the number of apices, net rhizome length and net number of internodes using a 330 day simulation. Simulated data were more variable than empirical data but simulated patterns of seagrass rhizome growth qualitatively matched empirical observations.

Conclusions This new model simulates the environmentally-dependant growth and senescence rates of a short-lived seagrass. It produces numerical and visual outputs that can be used to synthesise our understanding of plant functional processes relative to environmental parameters. It can also be used to assess the potential outcomes of management interventions like seagrass transplantation, thus, it is a useful management tool that would benefit from further refinement. It is freely available and easily adapted for new species and locations, although validation with more species and environments is required.

Key words
**Introduction**

Seagrasses are marine angiosperms which constitute a critical marine habitat but their range is declining globally (Orth et al. 2006; Waycott et al. 2009). They are a key component of marine food webs that stabilise sediments and sequester substantial amounts of carbon due to both their high productivity and propensity to trap organic matter (Orth et al. 1984; Kenworthy et al. 1989; Fourqurean et al. 2012). Their ecosystem services are financially valuable and they are the primary food of threatened species such as dugong, manatee and some sea turtles (Costanza et al. 1997; Green and Short 2003; Connell and Gillanders 2007; IUCN 2010). Global seagrass range is declining due to dredging, land reclamation, recreational boating, commercial fishing, contaminant discharge, nutrient enrichment of ambient waters, invasive species, global warming and poor land management (Fonseca et al. 2004; Orth et al. 2006; Connell and Gillanders 2007; Waycott et al. 2009; Sheppard et al. 2010; Short et al. 2011).

Understanding the environmental drivers of seagrass growth dynamics is critical for effective habitat management (Lee et al. 2007). Temperature is considered to be a major factor controlling seagrass seasonality because it affects the rates of seagrass photosynthesis and respiration (Phillips et al. 1983; Marsh et al. 1986; Lee et al. 2005, 2007). The influence that environmental drivers have on plant growth and senescence often involves complex interactions which can vary within and between species. Studying these relationships empirically is often complicated by logistical difficulties and high cost.

Computer simulation growth models are a proven tool for assessing and managing seagrasses. Numerical models have been used to help understand the function of seagrass meadows and to predict human impacts (Wetzel and Neckles 1986; Fong et al. 1997; Best et al. 2001; Newell and Koch 2004). Numerical models were improved for some applications by developing spatially-explicit representation of seagrass growth. Spatially-explicit modelling helps users to simulate and “observe” developmental progress which may be logistically difficult or temporally impossible to record empirically (Fonseca et al. 2004; Sintes et al. 2005). Some earlier spatially-explicit simulations of seagrass growth used a cell in-filling technique whereby occupied and unoccupied cells of an underlying grid were assigned different colours. Range expansion or contraction was represented by a change in the colour of the grid cells and this approach was effectively used to predict recovery times for damaged meadows and for observing the development of slow-growing seagrass reefs which take centuries to
develop (Fonseca et al. 2004; Kendrick et al. 2005). However, the scale of these simulations was limited to whole plants or meadows and the subsequent development of functional structural plant models (FSPMs) allowed users to simulate growth and senescence at much finer biological levels.

Functional-structural plant models allow users to assess plant developmental responses to the underlying biological and physical drivers of biomass change (Godin and Sinoquet 2005; Dejong et al. 2011). Users of FSPMs can define rules for multiple levels of biological structure, such as the function and structure of cells, branches or plants, to predict higher level outcomes, such as the development of branches, plants or meadows respectively (Godin and Sinoquet 2005; Hanan and Prusinkiewicz 2008; Dejong et al. 2011). The clonal growth of seagrasses is well suited to FSPMs and lower-level components are typically rhizome segment (internode), rhizome growth rate, branching frequency and branching angle (Sintes et al. 2005, 2006, 2007; Brun et al. 2006). Brun et al. (2006) and Sintes et al. (2006) built influential FSPMs using this clonal seagrass structure. Sintes et al. (2007) developed a spatially-explicit model for seagrasses that incorporated rhizome branching, mortality of rhizome apical meristems and internal signalling to represent dominance of some apical meristems over others. (Renton et al. 2011) designed and applied a spatially-explicit FSPM to identify the optimal planting arrangement for transplanting the slow-growing *Posidonia australis* Heck. However, at commencement of this study, no spatially-explicit FSPM had been reported that simulated both growth and senescence cycles and this is critical for simulations of short-lived seagrasses.

This study aimed to extend current seagrass models by developing a spatially-explicit FSPM for short-lived seagrasses that included a mechanistic link between environmental drivers and seagrass productivity, including both growth and senescence. We wanted the model to help users test their understanding of the environmental drivers of seagrass seasonality and also to predict the potential outcomes of management interventions. We wanted to test the model by applying it to a shallow subtidal population of the seagrass *Halophila stipulacea* (Forsk. Aschers. 1867) from the western Persian Gulf because this population exhibits rapid biomass response to the marked seasonal differences in physical and chemical water quality which it experiences. This population was thus ideal for testing whether our model could successfully integrate data on lower-level growth processes (at the plant component level) to predict higher-level behaviour (at the level of whole plants). Finally, we
wanted the model to be easily re-parameterised to represent other seagrass species and environmental conditions.

Methods

Model overview

The stochastic spatially-explicit functional-structural model simulates the dynamics of seagrass growth and productivity in response to environmental drivers that vary over time. The two key components of the model are apices (live apical meristems) and internodes (individual rhizome segments - as a real seagrass rhizome grows, its leaves are encased in a leaf sheath which encircles the rhizome, once the leaf sheaths senesce, they leave a clearly marked scar on the rhizome which defines the limits of an internode). The model simulates the branching structural development of seagrass plants by representing how each growing apex produces new internodes, leaves and additional apices over time. The number of initial apical meristems in the simulated plot area, the plot area dimensions and the duration of the simulation is defined by the user and is limited only by computer power. The structure and behaviour of the simulated seagrass is defined by a series of rules regarding branching pattern, internode angle and internode length. This version of the model mechanistically links seagrass growth and senescence rates with a locally relevant environmental parameter by assuming a linear relationship between the environmental parameter and the rate of rhizome growth and senescence. If the environmental parameter varies unimodally throughout the year, this will cause a corresponding unimodal trend in total rhizome length over time. Whilst this linear relationship drives the rate of change in total rhizome length, influences on apex survival such as may occur due to bioturbation, algal smothering or thermal inhibition can also be simulated by acting directly on apical meristem mortality, rather than by affecting the growth or senescence rate itself. Meristem death in this version of the model is primarily determined stochastically according to a base probability but the probability of mortality can be modified at certain times throughout the simulation to represent temporary effects such as storms, herbivory or competition.

Model implementation

The model is implemented in the open-source, platform-independent and freely downloadable statistical computing and graphics software package ‘R’ (R Core Team 2013). Two comma separated values (CSV) files contain parameterisation data which describe seagrass growth habit and a third CSV file provides the environmental data.
The CSV format was selected because it is broadly recognised and easily adjusted using common data management software such as Microsoft Excel. This makes it easier for operators with little or no computer programming experience to re-parameterise the model for new species and locations, a key aim of this project. Before starting the simulation, operators adjust the data in the CSV files to represent the lower-level aspects of growth habit of their case study species, define the environmental conditions of their case study location, set the simulation duration and the size of the area or empirical plot to be represented and define the initial number of apical meristems within the defined area.

**Case study species**

The model was parameterised to represent *Halophila stipulacea* (Forsk.) Aschers because this species responds rapidly to changes in environmental conditions and thus provided a good first case study for developing a model with a mechanistic link between seagrass productivity and environmental conditions. *Halophila stipulacea* is a small seagrass naturally occurring in the western Indian Ocean from Mozambique to south-western India (den Hartog 1970). It is an invasive species in the Mediterranean and Caribbean Seas where it was initially introduced via commercial and recreational boating activities and then expanded its range by sexual and vegetative reproduction (Lipkin 1975; Ruiz and Ballantine 2004; Willette and Ambrose 2012).

According to observations of plant growth and structure derived from field sampling conducted in Sumaisma Bay, Qatar (25°55’ N, 51°29’ E), leaf-bearing shoots were produced from apical meristems on rhizomes buried approximately 5 mm below the surface of the seabed. Apices produced two elliptical leaves, each flanked by a temporary leaf scale. Mean internode length was 9.7 mm (± 6.5 mm). The direction of each new internode generally alternated from the previous internode by 20° (± 22°). Branching angle was 87° (± 20°) and there was an 84% probability that branches would be produced on alternate sides of the parent stem. A single root was formed on each internode but persisted to maturity on only 52% of internodes. Surviving roots reached a mean length of 25 mm (±16 mm). At its mean maximum growth rate, a new internode with leaf scales, leaf pair and root was produced every 6.1 days (n=10) but this was as quick as 2 days. Mean apical density recorded from small, isolated stands of 100% cover in May 2012 was up-scaled to derive a m⁻² value of 1120 apices per m² (± 560, n=10). Senescence of the oldest part of the rhizome occurred concurrently with new growth at the rhizome apex throughout the year. This pattern of senescence resulted in
separation of branches with each branch forming a new independent plant and thus constituted an important, novel structural feature for our model. Most spatially-explicit plant models either do not include senescence or they have been developed for perennial species, where any senescence included in the model occurs from the loss of apical meristems, that is, shoot mortality (Fernández et al. 2011; Sarlikioti et al. 2011; Renton et al. 2011).

Case study location

The Persian Gulf is an epicontinental sea located between 24°N to 30°N and 48°E to 57°E which experiences minimal water exchange with the Indian Ocean and net evaporation due to high solar radiation coupled with negligible freshwater input (Purser and Seibold 1973). Sumaisma Bay is a shallow, east facing bay with mangroves, intertidal mudflats and subtidal seagrass meadows. Salinity at the study site remained above 40 PSU and temperature ranged between 7°C in winter to 40°C in summer. Sampling was conducted at a site with mean water depth of ~0.2 m below chart datum that is considered to be broadly representative of other shallow seagrass habitat throughout the western Gulf (Price and Coles 1992). The high seasonal variability of environmental parameters experienced in Sumaisma Bay made it an ideal site for parameterising a model of the growth and senescence of seagrass to understand how it is influenced by environmental factors.

Model details

In the simulation, each apex grows across the seafloor largely independently of other apices, producing new apices, internodes and leaves as it grows. Growth and structural development depends on the values specified for model parameters (Table 1 and Table 2). Growth rate is controlled by the user-specified influence of environmental data, which in our case study was a linear relationship between growth rate and temperature. The model produces a new internode when the cumulated value of the environmental variable reaches the user-specified required trigger value, represented by \( DDpernode \). Once a new node is produced, the cumulative value of the environmental variable is reset and accumulation recommences. The length and growth direction of each new internode is determined stochastically by drawing from normal distributions with means and standard deviation defined by the four model parameter values \( \text{len.mean}, \text{len.sd}, \text{nodeanglemean}, \text{nodeanglesd} \).
Sometimes a new apex is produced at the same time as a new internode. These new apices produce new branches which grow out from the parent stem. Whenever a new apex is produced, the number of internodes that it will produce before it branches again is determined stochastically by drawing from a normal distribution defined by the parameters \textit{count.mean} and \textit{count.sd}. To allow for alternate branching structures, the side of the parent stem to which a new branch will grow is determined stochastically, with the probability that the branch will be on the opposite side to the previous branch defined by the parameter \textit{branchaltprob}. The angle of the branch relative to the parent stem is also determined stochastically, drawn from a normal distribution defined by the parameters \textit{branchanglemean} and \textit{branchanglesd}.

All new nodes produced have a leaf attached to them and each leaf has a pre-determined life-span defined by the model parameter \textit{leaf.duration.days}. Leaves do not influence plant function but have been included for visualisation purposes. Leaf life span does not vary between leaves.

The model assumes a fixed minimum chance of apex mortality at each time step, which is defined by the model parameter \textit{Pbudmort} and occurs independently of environmental factors. It is also assumed that crowding or competition for light and other resources increases the chance of mortality when an apex has more other apices in its vicinity. Mortality due to crowding is simulated using two parameters: \textit{radforcount} defines the area surrounding an apex to consider and \textit{maxnum} represents the approximate maximum number of apices which can occur within this area. For each apex, at each time step, the number \( n_{\text{other}} \) of other apices with a radius of \textit{radforcount} is calculated, and then the probability of mortality is then calculated according to this equation:

\[
\text{pmort} = \text{Pbudmort} + \left( \frac{n_{\text{other}}}{\text{maxnum}} \right)^3 \times (1 - \text{Pbudmort}),
\]

where \( \text{pmort} \) is the probability of mortality for the apex at this time step. Whether or not mortality of that apex occurs at that time step is then determined stochastically according to the calculated probability. This ensures that as the number of other apices within \textit{radforcount} of an apex approaches \textit{maxnum}, then probability of mortality approaches one, ensuring that apex/bud density does not exceed \textit{maxnum}. Increased likelihood of apical mortality due to temporary or stochastic influences such as storms, competition or other factors can be represented directly in the model code; this is how we represented the impacts of crab burrowing and algal smothering described later.
Senescence proceeds from the base towards the tips of the branching structure. The oldest internodes senesce first, resulting in gradual isolation of branches from the parent stem. The time required for senescence of an internode is also mechanistically linked to environmental data. The senescence rate is defined by the equation:

$$R_s = d_b + (d_{mx} - d_b) \times \frac{1}{1+\exp(d_{tr}(E-E_t))}$$

where $R_s$ is senescence rate, $d_b$ is the minimum or base senescence rate (base.dieback), $d_{mx}$ is the maximum senescence rate (max.dieback.perday), $d_{tr}$ is the rate of transition between the maximum and minimum senescence rate (dieback.transition.rate), $E$ represents the environmental value on that day of simulation and $E_t$ represents the environmental value around which the transition is centred (dieback.transition.value).

For example in our case study, the maximum senescence rate occurs on days when water temperature is below the dieback.transition.value. For every degree above the dieback.transition.value, the senescence rate decreases at a rate determined by the value of dieback.transition.rate until it approaches base.dieback, and for every degree below the dieback.transition.value, the senescence rate increases in a similar way until it approaches max.dieback.perday.

Model parameterisation data are included in the files ‘basicparams.csv’ and ‘byorderparams.csv’, and the environmental data that drives the simulation is included in ‘envirodata.csv’. Species-specific data concerning internode lengths and the number of internodes between branching points is contained in ‘byorderparams.csv’. Because some seagrasses exhibit structural and functional differences between successional branches (Renton et al. 2011), users can enter different values describing the number of internodes and internode lengths for up to four branch orders into this file. The other parameter file ‘basicparams.csv’ contains general parameters controlling structural geometry, senescence, biomass and mortality.
Table 1: List, description and values of model parameters sourced from field sampling and used for parameterisation of the model for *H. stipulacea* in Sumaisma Bay, Qatar.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>Description</th>
<th>H. stipulacea value used</th>
</tr>
</thead>
<tbody>
<tr>
<td>radforcount</td>
<td>Radius for counting apical density</td>
<td>50 mm</td>
</tr>
<tr>
<td>maxnum</td>
<td>Maximum number of apices within the <em>radforcount</em> area</td>
<td>9</td>
</tr>
<tr>
<td>nodeanglemean</td>
<td>The mean angle of internode growth compared to the alignment of the previous internode. Node angle alternates, producing a zigzag growth pattern</td>
<td>20°</td>
</tr>
<tr>
<td>nodeanglesd</td>
<td>Standard deviation of the angle of internode growth</td>
<td>22°</td>
</tr>
<tr>
<td>branchanglemean</td>
<td>The mean angle at which the branch grows out from the parent branch</td>
<td>87°</td>
</tr>
<tr>
<td>branchanglesd</td>
<td>Standard deviation of the angle of branching</td>
<td>20°</td>
</tr>
<tr>
<td>branchaltprob</td>
<td>Probability of a branch growing on alternating sides of the parent branch</td>
<td>0.84</td>
</tr>
<tr>
<td>base.enviro.value</td>
<td>The minimum reported value for the environmental driver of growth which was water temperature in this case study.</td>
<td>13°C</td>
</tr>
<tr>
<td>DDpernode</td>
<td>The number of degree days required to produce one internode.</td>
<td>112</td>
</tr>
<tr>
<td>Pbudmort</td>
<td>Random probability of apical death</td>
<td>0.05</td>
</tr>
<tr>
<td>biomass.root.pernode</td>
<td>Mean mass of a root per internode (mg)</td>
<td>0.95</td>
</tr>
<tr>
<td>biomass.internode.pernm</td>
<td>Mean rhizome biomass (mg mm⁻¹)</td>
<td>0.38</td>
</tr>
<tr>
<td>biomass.leaf.per.node</td>
<td>Mean biomass of a leaf pair (mg)</td>
<td>7</td>
</tr>
<tr>
<td>leaf.duration.days</td>
<td>Estimated persistence time of a leaf (days)</td>
<td>25</td>
</tr>
<tr>
<td>max.dieback.perday</td>
<td>Maximum rate of internode dieback (number of internodes apex⁻¹ day⁻¹) applied from the oldest internode</td>
<td>0.26</td>
</tr>
<tr>
<td>base.dieback</td>
<td>Minimum internode dieback rate applied year round from the oldest internode</td>
<td>0.105</td>
</tr>
<tr>
<td>dieback.transition.rate</td>
<td>The rate of transition from <em>max.dieback.perday</em> to <em>base.dieback</em></td>
<td>0.1</td>
</tr>
<tr>
<td>dieback.transition.value</td>
<td>The value of the environmental parameter at which dieback rate transitions from <em>max.dieback.perday</em> to <em>base.dieback</em></td>
<td>&gt;20°C</td>
</tr>
</tbody>
</table>
Table 2: A description of branch order parameters and corresponding values used for parameterising the model to represent *Halophila stipulacea* in Sumaisma Bay, Qatar. No branch order differences were observed in this case study so the mean and standard deviation values provided here were used for all branch orders.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>Description</th>
<th><em>H. stipulacea</em> value used</th>
</tr>
</thead>
<tbody>
<tr>
<td>len.mean</td>
<td>Mean internode length</td>
<td>9.7</td>
</tr>
<tr>
<td>len.sd</td>
<td>Standard deviation of internode length</td>
<td>2</td>
</tr>
<tr>
<td>count.mean</td>
<td>Mean number of internodes between branches</td>
<td>2</td>
</tr>
<tr>
<td>count.sd</td>
<td>Standard deviation of the number of internodes between branches</td>
<td>2</td>
</tr>
</tbody>
</table>

**Model output**

The model produces a two-dimensional image showing the growing structure of the plant(s) (Figure 1). Simulated seagrass can grow beyond the designated visualised plot area; there is no limit on how far apices can grow. This means that apices can grow back into the visualised plot area from outside the plot area. It also means that the simulation will continue until the user-defined run duration is completed or until all apices have senesced, regardless of whether live apices appear within the visualised plot area. For all simulations in this paper, a visualised experimental plot area of 300mm x 300mm was used.

At completion of each time step the model records the number of apices, internodes, rhizome lengths and biomass. Biomass is calculated based on user-defined values representing the mass of each plant part, which is multiplied by the number of each plant part within the user-defined plot area. Upon completion of the model run the record is output to a csv file which is automatically saved in the user-specified file location.

**Model parameterisation**

Morphological data for *H. stipulacea* were collected by conducting detailed measurements of *H. stipulacea* in a total of 50 transplanted and reference seagrass plots at ~2 month intervals between 26 June 2010 and 21 May 2011. A further 10 seagrass plots were transplanted on 5 April 2011 and sampled on 20 April 2011 and 21 May 2011 to obtain detailed growth rate data for spring 2011. Further details of field survey methodology and project design are provided in Chapter 2 of this thesis (The influence
of environmental factors on Halophila stipulacea growth dynamics and transplantation in Qatar). The following descriptors of plant morphology were sampled in the field (with the corresponding model parameter name provided in brackets): internode angle (nodeanglemean, nodeanglesd), internode length (len.mean, len.sd), branch location (count.mean, count.sd), branch angle from the parent stem (branchanglemean, branchanglesd, branchaltprob), leaf presence or absence (leaf.duration.days), leaf length, and location of apical meristems. The change in the total number of internodes in a seagrass plot area between sampling events was used to derive values for parameters max.dieback.perday, base.dieback. Data were recorded on DuraRite© underwater paper which was transcribed into electronic spreadsheets upon return to the office. Biomass data were collected by harvesting five of the transplanted plots at ~2 month intervals. Biomass samples were separated into three categories, namely leaves, rhizomes and roots. Mean and standard deviation was determined for mass mm\(^{-1}\) and length to parameterise biomass.rootpernode, biomass.internode.permm, biomass.leaf.per.node for this case study. Water temperature was selected as the environmental driver of growth for this case study because it is a key influence on seagrass seasonality (Lee et al. 2007), it is simple to measure and, unlike light irradiance data, the logged data were not confounded by low levels of biofouling. Also, temperature is commonly used as the driver of growth in crop growth models through applying the concept of degree days which was replicated here. Water temperature was logged every 30 minutes of the sampling program using a Hoboware© temperature pendant (UA-002-64) which was installed 100mm above the seabed. The temperature logger failed between 17 February and 4 April 2012 and missing data were estimated by linear interpolation. Temperature data were used for base.enviro.value and was coupled with the net change in the number of internodes between sampling events to derive values for parameters DDpernode and dieback.transition.value. Values for Pbdmort and dieback.transition.rate were estimated based on observation. Apical mortality was not directly related to temperature but increased by approximately 1% in summer because of bioturbation by crabs and by approximately 5% in winter due to burial by decomposing macroalgae. To account for crab bioturbation, an additional apical mortality factor of 1% above the base probability of apical mortality was simulated when water temperature exceeded 28°C and to account for macroalgal smothering, apical mortality was increased by 5% when water temperature fell below 20°C. Because algal smothering was not observed when water temperature was below
20°C in autumn, the additional 5% apical mortality was applied only between days 190 to 300 of the simulation.

Model validation

In order to validate the model, each individual transplanted and reference seagrass plot was simulated for the same duration as the empirical sampling program, and simulation results were compared to empirical data for each corresponding plot. This validation method tests whether the model could successfully integrate lower-level processes and values to predict higher-level outcomes. That is, observed values regarding component-level aspects of plant morphology such as internode length, angles and branching frequency and direction were used in parameterising the model, and the parameterised model was then used to predict the structure and function of entire shoots and the number of apices, number of internodes and total rhizome length in a plot. These higher-level outcomes thus arose as emergent properties of the parameterized model, rather than being directly represented. Our validation consisted of testing whether these emergent characteristics of the model matched the corresponding characteristics of the real plants.

The number of initial apices in each simulation was as close as possible to the actual number of initial apices recorded in the field, with the constraint that the model assumes initial apices are distributed in a grid. No more than five initial apices were modelled in a single row or column of the grid to avoid excessive apical death due to crowding and this may have caused some deviation from field data in those few plots where this situation occurred. Where the initial number of apices was an odd number greater than five, the next closest allowable number of apices was used, alternating between the next highest followed by the next lowest. For example, if two plots contained seven initial apices, the initial number of apices was six in the first simulation (3 columns on each of 2 rows) and eight (4 columns by 2 rows) in the second simulation. Paired t-test was used to test whether there was a significant difference between the observed and simulated values for net rhizome length, net number of apices and net number of internodes.

Results

The graphical output of the parameterised model representing the dynamic structural growth and development of the seagrass plants qualitatively matched the growth patterns of H. stipulacea observed at the study site (Figure 1). There was a reasonable match between empirical and simulated results over the 330 day simulation for net
number of apices, net rhizome length and net number of internodes, although simulated data were generally more variable than observed data (Figure 2). Paired t-test indicated no significant difference between the observed and simulated values.

![Day 1](image1.png)
![Day 110](image2.png)
![Day 220](image3.png)
![Day 330](image4.png)

Figure 1: Two-dimensional snapshots illustrating the simulated growth of two initial apical meristems at 110 day intervals for a period of 330 days, where the visualised area represents an experimental plot. Grey lines represent decayed rhizomes, green lines represent live rhizomes, green circles represent leaves and red circles represent growing apical meristems within a 300 mm by 300 mm plot area. Both initial apices out-grew the plot area and the left apex subsequently re-entered the plot area.
Figure 2: Validation results for net number of apices, net rhizome length and net number of internodes. The boxes represent the interquartile range for observed and modelled plants over 330 days. Where: ^ data collected from transplants planted on 26 June 2011, * data collected from transplants planted on 5 April 2012. The whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box, while data points more than 1.5 times the interquartile range are shown individually as open circles.

Discussion

The good match between simulated and empirical data observed during model validation was encouraging. The model adequately simulates seasonal variability (Figure 2), however, the greater variability in the simulation requires further investigation and model refinement. Inaccuracies in the simulation results may be explained by the simplistic representation of plant functional-structural responses to environmental conditions which was used in this case study. The model uses a linear
function to predict the relationship between seagrass growth dynamics and water temperature as the basis for growth. Whilst environmental influences of bioturbation and macroalgal smothering have been overlaid on this to simulate some biological influences, it is possible that the underlying relationship between growth and abiotic environmental factors is non-linear and (Lee et al. 2007) and there may be negative feedbacks that restrict growth during summer which have not been applied in the model. The linear relationship used as the basis for simulating growth was developed using the mean of a small sample of maximum growth rates (n=5) coupled with a single water temperature value. A more accurate relationship might be derived in future with the use of a multiple regression formula if more data were available. Similarly, the formula for senescence is based on qualitative observation of seasonal changes which would benefit from more accurate quantitative descriptions derived from more frequent sampling. Thus, although this version of the model effectively represents seagrass growth relative to environmental seasonality, the accuracy of the model might be improved by a more accurate and possibly multifactorial description of the environmental drivers of growth and senescence. The high variability in simulation results may be explained by the stochastic nature of the simulation. It appears that these processes may be less stochastic in reality than modelled, possibly due to stabilising feedback processes that decrease growth, branching and/or apex survival when plants are larger.

This FSPM was designed so that it is simple to adapt for simulating a range of seagrass species and environments. The mechanistic link between plant function and environmental parameters is a key model component which simplifies reparameterisation of the model, compared to similar earlier seagrass FSPMs where models were parameterised for a specific set of environmental conditions that did not allow for seasonal variability (Renton et al. 2011). This mechanistic link also constitutes a useful development of spatially-explicit, FSPMs for seagrasses because it can be used to predict and test our understanding of seagrass seasonality. We wanted the model to be widely available and easily re-parameterised so the model was written using the freely available computer graphics and statistics package ‘R’ (R Core Team 2013) and most parameterisation data is entered into csv spreadsheets that can be easily modified in any of the widely used spreadsheet programs. Since R is a relatively simple programming language and environment that is freely available and increasingly widely used, it should also be relatively easy to recode aspects of the model that cannot be adapted as required through simple manipulation of parameter values. We hope that this will facilitate further use, validation and development of the model.
The validation we conducted showed that our model successfully integrated lower-order values and processes to predict higher-order outcomes, and we would expect the mechanistic nature of the model to give it some predictive value in different locations and environments, but further data collection and validation would be needed to properly test this. Parameterisation data were derived from vegetative fragments or seagrass growing at the fringes of an existing meadow and therefore, the model may not accurately represent seagrass behaviour in an established meadow. Field investigations identified rare, isolated stands of tightly branching seagrass with short internodes and high apical density which persisted through winter. The model did not produce any simulations which represented this growth form and this demonstrates the importance of further model refinement. Nonetheless, to account for the rare instances where simulated *H. stipulacea* may attain the maximum apical density observed in these isolated patches, variables have been included in the model to allow for apical death due to crowding, thus limiting maximum apical densities to those observed in the field and ensuring unrealistically high densities are not produced. The model improves on previous seagrass FSPMs (Renton et al. 2011) by representing senescence and dependence on environmental conditions, but similarly to Renton et al. (2011) the model has been designed and validated for seagrass species which do not have a vertical rhizome growth strategy and would thus require further development to account for a three-dimensional growth pattern.

The visual representation of the dynamic branching structure of seagrass rhizomes provided by the model helps stakeholders quickly appraise the potential outcomes of management interventions such as seagrass transplantation. This simplifies communication of potential project outcomes to stakeholders who may have a limited understanding of ecological processes. For example, in the case study reported here, the model clearly demonstrates that transplantation of *H. stipulacea* in the Persian Gulf would be unlikely to produce a persistent meadow by vegetative reproduction, because most transplanted fragments would completely senesce by the end of the first winter. This outcome is pertinent for proponents and environmental authorities when considering the potential impacts and mitigation measures of coastal construction projects and it is relevant to two large-scale coastal construction projects in Qatar where seagrass transplantation was recently conducted (Seagrass Watch 2009; Al Jamali Environmental Consultancy 2013).
The potential uses of the model are extensive. In its current state the model is useful for scientific purposes such as understanding how local-level processes result in emergent higher-order outcomes. It is also useful for more applied purposes such as forecasting potential impacts of environmental changes on seagrass productivity or predicting seagrass transplantation outcomes with different planting densities or arrangements (Renton et al., 2011). With further testing and development, this model could be linked to hydrodynamic models at various spatial scales and used in environmental impact assessments to assess potential ecological impacts (Verduin and Backhaus 2000; Burkhard et al. 2011). The model could also be developed to assist with invasive species management. For example, a range of chemical and mechanical options were trialled for managing the invasive marine alga *Caulerpa taxifolia* in Australia (Glasby et al. 2005). With an understanding of the likely physiological response produced by the control method may have on the invasive species, the potential outcomes of each control method could be simulated to help appraise their relative effectiveness prior to implementation, potentially improving project outcomes and reducing unnecessary effort and environmental impact.

This paper presents an important progression in the field of functional–structural plant modelling for seagrasses and provides an easily adapted tool to effectively assess and manage seagrass habitat.
Literature cited


General Discussion

The investigation reported in this thesis has provided a detailed description of *H. stipulacea* growth dynamics relative to the extreme environmental seasonality of the Persian Gulf. It has identified important biological influences on seagrass growth dynamics in the Gulf and has assessed the likely outcomes of *H. stipulacea* transplantation in Qatar for reference by natural resource managers, consultants and developers. It has also led to the development of a new, FSPM parameterised using detailed *H. stipulacea* data. The model has been designed so that it is freely accessed and easily re-parameterised for other seagrass species occurring in environments other than that reported here.

*Halophila stipulacea seasonality relative to environmental factors*

Light and temperature are commonly identified as the drivers of seagrass growth and whilst both parameters were important in this study, the relationship between growth and temperature was not as strong as expected. This may be due to a number of factors including the relatively long duration between sampling events (2 months) for this quick growing and largely short-lived population. Exceedance of the published thermal tolerance limits for seagrasses of the tropics (32°C) and for those of the Gulf (37°C) did not appear to negatively affect seagrass growth in the shallow, intertidal population reported here, although this population may be genetically adapted to high summer temperatures than other populations as the high summer temperatures recorded in this study were not anomalous (Price and Coles 1992; Lee et al. 2007; Procaccini et al. 2007; Erftemeijer and Shuail 2012). The conduct of laboratory trials that measure growth and senescence rates relative to controlled environmental conditions would be a useful progression of this study that would improve understanding of the various influences on seagrass productivity, thus improving the capacity for effective management. Experimental laboratory trials would be a useful component of further study.

The observed predominantly short-lived nature of *H. stipulacea* stands sampled in this study was also observed in the broader meadow, where few small, dense stands of tightly clustered rhizomes with short internode distances and small leaves persisted through winter. The small leaves suggest that light limitation was not the principal factor limiting growth in winter, as populations of *H. stipulacea* occurring elsewhere in light limited conditions tend to grow large leaves in an effort to maximise light capture.
efficiency (Lipkin 1979b). This suggests that further information is required to accurately understand the drivers of seagrass seasonality in the Gulf, but that light and temperature are likely key influences in addition to the biological influences of bioturbation and algal smothering reported in this thesis. Any further study of this type should be conducted over sampling intervals of approximately 2 weeks.

The evidence for *H. stipulacea* seasonality provided here goes some way to clarifying the question of seagrass seasonality in the Gulf. Price and Coles (1992) did not identify any correlation between seagrass biomass and season in their 20 month investigation of all three seagrass species that occur along the eastern coast of Saudi Arabia. Their findings may be partially explained by the spatial heterogeneity of seagrass meadows and their lack of permanent survey reference point when conducting repeat sampling. From general literature regarding seagrass seasonality it seems likely that *H. ovalis* and *Halodule uninervis* in the Gulf exhibit broadly similar seasonality to the *H. stipulacea* results reported here (Lee et al. 2007). However, the degree of seagrass growth and senescence response to environmental factors likely differs between species and populations. For example, less marked seasonality would be expected for populations which occur in deeper waters where environmental conditions are less variable. Similarly, different growth habit to that reported in this study is expected for *H. stipulacea* populations occurring elsewhere in its global range, such as in the more temperate waters of the Red Sea or Mediterranean Sea. Given the high genetic diversity and morphological plasticity of *H. stipulacea* (Procaccini et al. 1999), seagrass management strategies should be informed by the results of local investigations.

Finally, the findings here are derived from studying *H. stipulacea* growing in isolated patches or at the fringes of larger patches. *Halophila stipulacea* reportedly occurs in monospecific meadows elsewhere in its range although this was not the case at the study site and removal of other species from experimental plots may have affected results. Thus, the seagrass function and structure reported here may not represent that of established meadows.

**Transplantation**

Seagrass transplantation did not affect the survival of *H. stipulacea* shoots, principally because the transplanted and reference populations were predominantly short-lived, exhibiting rapid growth in spring and rapid senescence in winter. Clearly transplantation of short-lived populations should not be expected to result in persistent meadows and is thus likely to be of little value if conducted to offset the environmental impacts of land
reclamation projects, as recently conducted in Qatar (New Doha International Airport 2013). An extensive seagrass transplantation project has recently been conducted as a condition of development consent for the construction of the New Port Project in Qatar. Whilst *H. stipulacea* populations growing in deeper waters are less likely to exhibit such marked seasonality as those in shallow, subtidal environments, this study demonstrates the need for appropriate assessment of the local seagrass populations prior to the stipulation of transplantation as a condition of development consent. Thus, it is hoped that the findings reported here may have significant implications for the assessment and conditioning of development applications in the Gulf. Transplanting *H. stipulacea* in some locations may be appropriate for the purposes of compressed succession, that is, for the purpose of stabilising a restoration site for subsequent natural recolonisation by the climax species (Fonseca et al. 1994). Transplanting *H. stipulacea* as part of a compressed succession program may be appropriate in environments where it is seasonally persistent and where this process of natural succession occurs.

Any *Halophila stipulacea* transplantation should be conducted during optimal environmental conditions to reduce stress on transplanted fragments. Optimal conditions for the population investigated in this study are high light irradiance and moderate to high water temperature, such as occur in spring and summer. However, *H. stipulacea* exhibits high morphological plasticity and has high genetic diversity between populations (Procaccini et al. 1999). Therefore, transplantation programs should be designed and implemented using local donor material where possible, based on the results of detailed local investigations, rather than relying on species-level generalisations.

Drifting macroalgal mats had a marked effect on seagrass senescence, particularly in late winter to early spring. Individual plots of transplanted and reference seagrass were identified in this study by driving numbered steel stakes into the seabed at the corner of each plot. Once macroalgae became detached and started drifting across the seabed, they became entangled in the protruding stakes. This likely caused additional concentration of drifting macroalgae over the study plots, compared to seagrass in the wider meadow. Marking transplants may thus have exacerbated the impact of macroalgal smothering, increasing senescence and delaying the commencement of rapid growth recorded in spring. Any future transplantation should use a labelling technique which reduces the risk of such entanglement.
The common global goal of rehabilitating areas of historical seagrass decline by transplantation is not an issue in Qatar as the principal driver of loss is new coastal development. However, in the event that rehabilitation of previously damaged areas is warranted, the seed-dependency of the Gulf species would likely be a useful feature to facilitate recolonization, such as by translocating sediment which contains viable seed.

**Functional-structural plant modelling**

The model developed in this study is a useful first step toward a fully functional and fully adaptable model for short-lived seagrasses. The model adequately simulated the growth and senescence of the *H. stipulacea* population which was the subject of this study, and in its current state it is a useful tool for assessing management options for *H. stipulacea* throughout its range. However, populations of *H. stipulacea* may exhibit marked functional and structural differences compared to the population reported here, and given the degree of morphological plasticity, the model should ideally be parameterised for each local population (Procaccini et al. 1999).

A better understanding of the multifactorial influence on seagrass growth dynamics and the possibility of including additional stabilising feedback processes are expected to reduce the variability in simulated results, which would be a useful improvement of the model. Based on the consensus that temperature, light and nutrients are the dominant drivers of seagrass productivity worldwide, initial investigations should extend to quantifying these influences on seagrass growth dynamics. Similarly, more accurate quantification of the effect of biological influences on seagrass apical mortality would help reduce the variability in the simulated seagrass growth by more accurately predicting the activity of crabs and smothering by macroalgae in winter. The importance of localised abiotic influences on seagrass apical mortality, such spatial variation in hydrodynamics, should also be investigated. Also, to demonstrate the full adaptability of the model, further validation with other seagrass species and environmental drivers is required. This process may reveal that additional ecological processes need to be incorporated into the model to fully achieve the desired adaptability.

With further development, the model may also be adapted for use with other clonal organisms which exhibit a horizontal growth strategy across the seabed. The invasive algae *Caulerpa taxifolia* has recently been the subject of intensive management to control its range in Australia (Glasby et al. 2005). The model discussed here may be useful for such investigations using information describing the species’ response to different environmental manipulations; simulations could be run to investigate how the
population of the invasive species will response to various management techniques, such as addition of highly saline water, thermal discharge or light reduction.

Finally, the model may be useful for predicting the impacts of climate change on the subject species. With detailed information about species response to environmental conditions, the environmental parameters in the model could be manipulated to simulate the expected biomass and growth under the forecast environmental conditions. Thus, it could potentially assist in understanding and managing biodiversity conservation, ecosystem productivity and carbon sequestration in a changing climate.

Literature cited


