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# Coastal retreat and improved water quality mitigate losses of seagrass from sea level rise

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## Abstract

The distribution and abundance of seagrass ecosystems could change significantly over the coming century due to sea level rise (SLR). Coastal managers require mechanistic understanding of the processes affecting seagrass response to SLR to maximize their conservation and associated provision of ecosystem services. In Moreton Bay, Queensland, Australia, vast seagrass meadows supporting populations of sea turtles and dugongs are juxtaposed with the multiple stressors associated with a large and rapidly expanding human population. Here, the interactive effects of predicted SLR, changes in water clarity, and land use on future distributions of seagrass in Moreton Bay were quantified. A habitat distribution model of present day seagrass in relation to benthic irradiance and wave height was developed which correctly classified habitats in 83% of cases. Spatial predictions of seagrass and presence derived from the model and bathymetric data were used to initiate a SLR inundation model. Bathymetry was iteratively modified based on SLR and sedimentary accretion in seagrass to simulate potential seagrass habitat at 10 year time steps until 2100. The area of seagrass habitat was predicted to decline by 17% by 2100 under a scenario of SLR of 1.1 m. A scenario including the removal of impervious surfaces, such as roads and houses, from newly inundated regions, demonstrated that managed retreat of the shoreline could potentially reduce the overall decline in seagrass habitat to just 5%. The predicted reduction in area of seagrass habitat could be offset by an improvement in water clarity of 30%. Greater improvements in water clarity would be necessary for larger magnitudes of SLR. Management to improve water quality will provide present and future benefits to seagrasses under climate change and should be a priority for managers seeking to compensate for the effects of global change on these valuable habitats.

*Keywords:* climate change, coastal ecosystems, multiple stressors, remote sensing, sea level rise, spatial modelling, species distribution, wave model

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## Introduction

Global change is causing significant alterations to the distribution and function of ecologically and economically important marine ecosystems such as saltmarshes, seagrass, mangroves and coral reefs (Alongi, 2002; Lotze *et al.*, 2006; Waycott *et al.*, 2009; Hoegh-Guldberg & Bruno, 2010). Seagrasses are marine flowering plants that form critically important ecosystems in coastal seas, providing food, shelter and nursery grounds for fish, invertebrates, turtles and dugongs (Coles *et al.*, 1987; Lanyon *et al.*, 1989; Beck *et al.*, 2001); sediment stabilization (Orth *et al.*, 2006); water filtration (Mcglathery *et al.*, 2007); and carbon sequestration (Nellemann *et al.* 2009; Fourqurean *et al.*, 2012). However, large-scale and rapid loss of seagrass of 7% $yr^{-1}$ since the 1990s, and the extinction of multiple species predicted in the coming century (Short *et al.*, 2011; Jordà *et al.*, 2012), has generated significant concern for their continued existence and provision of ecosystem services (Waycott *et al.*, 2009). Seagrasses grow in relatively shallow coastal seas, ranging from intertidal areas where they are influenced by desiccation and wave action (Fonseca & Bell, 1998), to a maximum depth of generally less than 10 m, due to their relatively high light requirements (Dennison, 1987; Duarte, 1991; Dennison *et al.*, 1993). Decreased water clarity due to nutrient inputs or sedimentation from coastal development and dredging has been largely responsible for losses to date (Waycott *et al.*, 2009; Short *et al.*, 2011). Both short and long-term stresses can impact seagrasses (Grech *et al.*, 2012); to understand the consequences of these stressors, it is necessary to focus

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on key drivers of seagrass distribution, including interactions amongst multiple stressors.

Sea level rise (SLR) of a metre or more (Vermeer & Rahmstorf, 2009; Nicholls *et al.*, 2011; Bamber & Aspinall, 2013) over the 21st century as a consequence of warming seawater and melting ice may contribute an additional challenge to these coastal ecosystems. SLR will increase water depth and so reduce the availability of light to seagrass. This is because light availability on the seafloor is inversely related to both water depth and the light attenuation coefficient, which is a function of the optical properties of water and constituents, such as suspended sediments. Given the high sensitivity of seagrass to irradiance, SLR has the potential to cause further decline in ecosystems already threatened by diminished water quality. Compared to other coastal ecosystems (e.g. Morris *et al.*, 2002; Kirwan & Murray, 2007; Traill *et al.*, 2011; Runting *et al.*, 2012), relatively little research has been conducted on the impact of SLR on seagrasses. Seagrass can respond to SLR via several mechanisms: (i) adaptation/acclimation to new conditions, (ii) migration into newly available regions, (iii) accretion of biological and sedimentary material vertically to keep position relative to sea level and (iv) loss, if conditions become unsuitable (Short & Neckles, 1999; Duarte, 2002; Waycott *et al.*, 2007). Predicted impacts of SLR on seagrass (Short & Neckles, 1999; Duarte, 2002; Waycott *et al.*, 2007; Collier & Waycott, 2009) have not been quantified empirically in field studies, likely due to lack of long and detailed time series of seagrass distribution and only a relatively small rise in sea level of 20 cm (Church & White, 2011) over the previous century. However, some key recent modelling studies based on *Zostera* spp. in North America (Kairis & Rybczyk, 2010; Carr *et al.*, 2012b; Shaughnessy *et al.*, 2012) have found the effects of SLR on seagrass to be variable and context dependent: both predicted increases or decreases in extent of seagrass have been reported (Kairis & Rybczyk, 2010; Shaughnessy *et al.*, 2012).

Identifying generalities in the management actions that could improve conditions for seagrass under rapid SLR would be extremely valuable. Importantly, whether seagrass establishes in newly inundated regions will be influenced by land use in adjacent areas (Waycott *et al.*, 2007). In highly developed urban areas, hardened shorelines will prevent inland migration of coastal habitats, a phenomenon known as ‘coastal squeeze’ (Nicholls, 2011). The potential magnitude of this effect has not been quantified for seagrasses in any region. Likewise, the impact of water clarity in the response of seagrass to SLR has not been quantified to date. Land use and water clarity may both be potentially influenced by management actions; therefore, quantifying their effect on seagrass distribution subject to SLR can inform conservation strategies. Furthermore, where interactions between global stressors such as climate change and local stressors such as water quality occur, the effects of the global stressors may potentially be mitigated through management of the local stressor (Crain *et al.*, 2008; C.J. Brown, M.I. Saunders, H.P. Possingham & A.J. Richardson, unpublished data). Therefore, an opportunity may exist to offset declines in seagrass due to SLR by improving water quality. To do so requires quantification of the relative effects of these two stressors. For management purposes, models of ecosystem response to SLR should ideally be spatially explicit, cover relatively large spatial scales, and incorporate the multiple relevant physical forcing factors.

The objectives of this study were to (i) develop a spatially explicit habitat distribution model of seagrass presence vs. absence using benthic irradiance and wave height as predictor variables, (ii) quantify the spatial and temporal effects of SLR on seagrass under realistic scenarios of SLR and incorporating sedimentary accretion and (iii) quantify the effects of coastal squeeze and water quality on abundance of seagrass under SLR. Moreton Bay, Australia, was used as a study site because it encompasses a wide variety of coastal habitats, ranging from relatively pristine wildlife refugia supporting abundant populations of endangered and threatened species, to turbid, highly impacted inshore regions where large-scale losses of coastal habitats have occurred historically as a result of human pressures. The results of the study are used to derive management recommendations for seagrass subject to SLR.

## Materials and methods

### *Study location*

Moreton Bay, Southeast Queensland, Australia (27°S, 153°E) is a 1500 $km^2$, mesotidal (~2 m), semi-enclosed estuarine embayment with average depth of 6 m, sheltered from the Pacific Ocean by Moreton and Stradbroke Island (Fig. 1). With a subtropical climate, the average annual rainfall is 1.2 m at Brisbane International Airport, of which 70% occurs during the wet austral summers from November to April (Australian Bureau of Meteorology, www.bom.gov.au). Prevailing winds are from the southeast during the cool, dry, austral winter and northeast in the warm, humid summer. Water temperature ranges from 15 to 28 °C throughout the year (www.healthywaterways.org).

Water clarity in Moreton Bay ranges from 0.1 m to 15 m, and is primarily affected by suspended sediments in run-off from five major catchments, which creates strong east–west gradients in water clarity (Dennison & Abal, 1999; Phinn *et al.*, 2005). The Brisbane and Logan rivers run through Brisbane, the 3rd largest city in Australia and the capital of Queensland, and drain agricultural and urban run-off into the inshore regions of Moreton Bay. Water clarity in shallow coastal embayments such as Moreton Bay is further influenced by

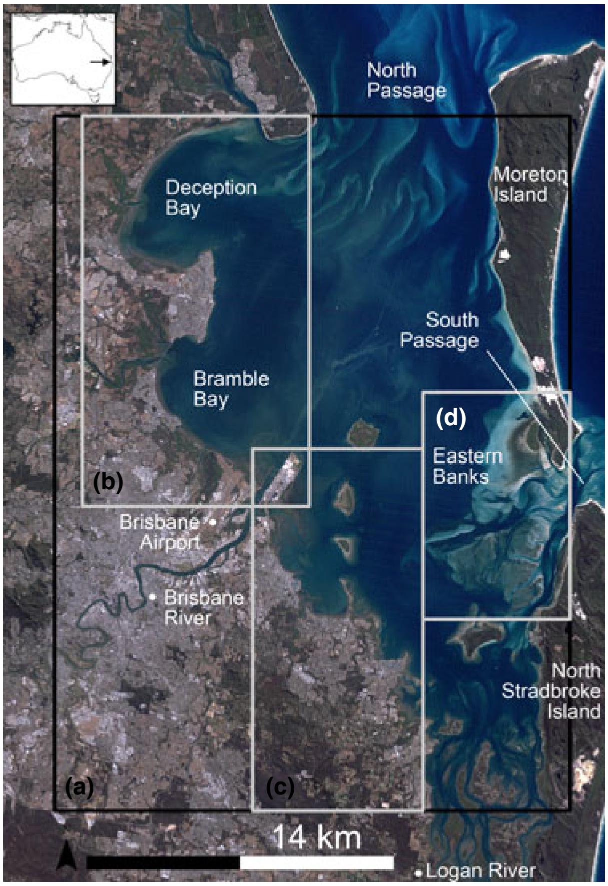


**Fig. 1** Landsat Five Thematic Mapper image from 27 July 2011 (Source: United States Geological Survey) of the study region in Moreton Bay, Southeast Queensland, Australia. Located adjacent to the metropolis of Brisbane – capital of Queensland, Australia's third largest city, and the fastest growing 'Mature' City in the world, Moreton Bay has extensive seagrass meadows, abundant populations of vulnerable and threatened species, a strong east–west gradient in water clarity, and existing and growing pressure from coastal development. The black box indicates the modelled area, and white boxes indicate subset areas used for regional analyses.

sediment re-suspension, which is largely due to wind driven waves, and their interaction with bathymetry (Carniello *et al*., 2011). Southeast Queensland has a population of over 3 million, and Brisbane is considered the fastest growing 'mature' city in the world (Jones Lang Lasalle, 2012). Circulation of water within the bay is clockwise, with oceanic exchange of clearer water occurring via North and South passages. Shallow bathymetry and limited exchange with the open ocean generate relatively long water residence times of average 45 days, particularly in the western Bay.

Coastal and marine habitats in Moreton Bay include seagrasses, saltmarshes, mangroves and mudflats, with limited areas of rocky and coral reefs. Seagrass meadows comprising six species (*Zostera muelleri*, *Cymodocea rotundata*, *Syringodium isoetifolia*, *Halodule uninervis*, *Halophila ovalis*, *Halophila spinulosa*) form extensive habitats of approximately 189 km$^2$ along the coastline of the western bay, through the channels of South Passage, and in the Eastern Banks (Roelfsema *et al*., 2009). Losses of seagrass, particularly in the north-western portion of the bay, have occurred historically in response to shoreline development (Hyland *et al*., 1989) and diminished water clarity (Abal & Dennison, 1996). To protect the significant ecological resources in Moreton Bay, including abundant populations of IUCN Red listed endangered Green sea turtles (*Chelonia mydas*) and vulnerable Dugongs (*Dugong dugon*), a network of marine parks was established in 1994 which underwent significant expansion and rezoning in 2009 (Anon, 2008).

## *Modelling overview*

The modelling procedure in this study comprised three steps, including the following: (i) creation and validation of a spatially explicit distribution model for seagrass vs. non-seagrass habitats, (ii) simulation of change in sea level and estimation of changes in distribution of seagrass habitat due to SLR and (iii) analysis of the effects of water clarity, sediment accretion and adjacent land use on distribution of seagrass in response to SLR (Fig. 2).

First, the probability of a location providing habitat suitable for seagrass was modelled as a function of significant wave height (defined as the average of the largest one third of wave heights), and the logarithm of percentage irradiance on the benthos. Second, incremental changes in the distribution of suitable habitat was simulated by modifying the digital terrain model according to SLR and sedimentary accretion, and then re-predicting habitat suitable for seagrass, at 10 year time steps from 2000 to 2100. Third, the influence of environmental parameters and management scenarios on total area of seagrass in response to SLR was examined: (i) using natural spatial gradients in water clarity and (ii) simulating changes in water clarity, sediment accretion and simplistic scenarios of land use in response to inundation.

The original modelled area of ocean consisted of 145 165 grid cells, with individual cell dimensions of 100 × 100 m, corresponding to a total area of 1452 km$^2$ (indicated by the black box in Fig. 1). Areas potentially suitable for seagrass were defined as seawater <0 m depth relative to mean sea level. Input data were manipulated to meet the model specifications of modelled area, grid cell size, projection and coordinate systems using ArcGIS® 10.0 (Esri Headquarters, Redlands, CA, USA), and model development and analysis were conducted using R 2.13.1. Following is a description of the input data and parameters, model construction, validation and analyses.

## *Input data and parameters*

Input data and parameters were compiled from multiple sources (Table 1) as described below.

*Seagrass distribution*. Seagrass presence vs. absence data were obtained from seagrass cover maps presented in Roelfsema *et al*. (2009) (Fig. S1a). These maps covered intertidal and shallow subtidal (<10 m) areas throughout Moreton Bay and

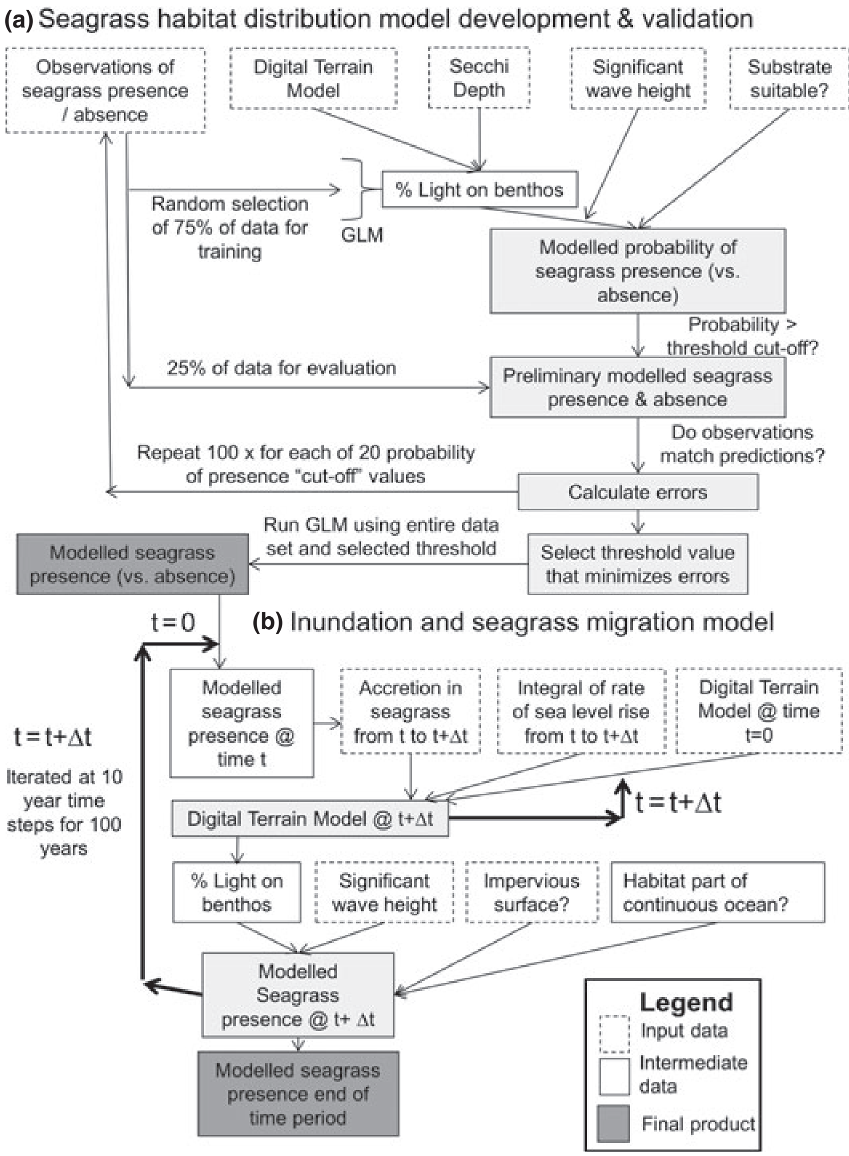


**Fig. 2** Work flow diagram for model of changes in seagrass distribution under sea level rise in Moreton Bay, southeast Queensland, Australia. (a) Seagrass distribution model development and validation; (b) Sea level rise inundation and seagrass migration model.

were derived from Landsat Thematic Mapper five images captured in June/July 2004 using coincident field surveys for classification, calibration and validation. In this study, seagrass was considered 'present' if seagrass cover of any species was >0%.

*Benthic substrates.* Benthic habitat data were obtained from the former Queensland Department of Environment and Resource Management (DERM, www.derm.qld.gov.au) (Fig. S1b). Benthic substrates were considered suitable for seagrass if they were sand or mud, and unsuitable if they were rock or coral.

*Digital terrain model.* A seamless digital terrain model for Moreton Bay and its coastline was constructed by combining 1 m resolution LiDAR-derived topographic data and near-shore bathymetric datasets (DERM) with 100 m resolution bathymetric data from the 3DGBR depth model (Beaman, 2010) (Fig. S1c). The high-resolution topographic terrain model was resampled to a 100 m grid size and mosaicked following Leon *et al.* (*In press*).

*Water clarity.* Secchi depth (m) was used as an indicator of water clarity. Field measurements of Secchi depth were obtained from the Healthy Waterways Ecological Health Monitoring Project (EHMP, www.healthywaterways.org). Monthly data were obtained from 61 stations located throughout the bay (Fig. S1d) for the 6 months prior to data collection of the seagrass maps, and averaged over time. A statistical model of Secchi depth based on Euclidean distance of the sampling

**Table 1** Data and processes used in modelling effects of sea level rise on seagrass in Moreton Bay, Southeast Queensland, Australia

| Data or process | Source | Spatial resolution | Cause of uncertainty | Uncertainty |
|---|---|---|---|---|
| Seagrass maps | Roelfsema *et al.*, 2009; | 30 m | Accuracy of classification procedure | Pixel-based image analysis percentage agreement value = 40–60% |
| Secchi depth | Ecosystems Health Monitoring Programme | 61 points in Moreton Bay – used to model Secchi depth at 100 m resolution | Averaging over 6 months; spatial interpolation | Large temporal variability, >80% spatial variability explained by model |
| Significant wave height | SWAN Model (this study) | 100 m | Averaging over time; errors in bathymetric data, assumptions about physical processes | 84% of variability in observed wave height explained by SWAN model |
| Terrain model | LiDAR; Beaman, 2010; | 100 m in ocean | Interpolation amongst bathymetric contour lines | Vertical uncertainty = ±0.5 m |
| Rate of SLR | Vermeer & Rahmstorf, 2009; | Spatially constant | Rate and magnitude of warming of climate; quantity of melting ice; local factors such as subsidence | Unknown. Large variability in estimated magnitude of SLR. Range of estimates = 0.2–2 m |
| Rate of accretion | C.M. Duarte, I.J. Losada, I. Hendriks, I. Mazarrasa & N. Marba, unpublished data | Spatially constant | Spatial, temporal, location specific, and ecological variation | Unknown |
| Conditions in newly inundated regions (light, waves) | Extrapolated or modelled from data in adjacent ocean areas | 100 m | Uncertainty in effect of inundation of terrestrial sediments on water clarity; potential for large-scale changes in geomorphology | Unknown |
| Impervious surfaces map | Lyons *et al.*, 2012 | 30 m | Accuracy of classification procedure, artefacts from aggregation, not accounting for future development | Object-based image analysis percentage agreement value for impervious classes = 92% |

stations from sources of turbid (rivers) and clear (open ocean, >30 m depth) water was developed, as these two factors are likely to influence water clarity in the region (Abal & Dennison, 1996; Phinn *et al.*, 2005). Water depth was also included since re-suspension by wind and waves is more likely in shallower water. A linear model of Secchi depth (m) as a function of these three factors, including all 2- and 3-way interaction terms, explained 86% of the variability in seasonally averaged Secchi depth (Adjusted $R^2 = 0.86$, $P < 0.01$, Table S1). Using the coefficients from this model, Secchi depth at all other locations <0 m in the bay was predicted (Fig. S1d).

*Benthic light availability.* At a given location, the irradiance $I$ (W m$^{-2}$ s$^{-1}$) at depth z is a function of the clarity and depth $z$ (m) of the water and is described by the following:

$$I(Z) = I_0 e^{-k_d Z} \tag{1}$$

where $I_0$ is the surface irradiance (W m$^{-2}$ s$^{-1}$) and $K_d$ is the diffuse attenuation coefficient (m$^{-1}$) representing water clarity. $I(z)/I_0$ can be simplified to % light available at depth $z$. $K_d$ can be estimated as a function of Secchi depth ($Z_{SD}$) according to the following:

$$K_d = \frac{\lambda}{Z_{SD}} \tag{2}$$

where the constant $\lambda$ is approximately 1.7 (Poole & Atkins, 1929).

*Significant wave height.* A synoptic map of significant wave height ($H_s$) was created using The Simulating WAves Nearshore (SWAN) (Booij *et al.*, 1999; Ris *et al.*, 1999; Holthuijsen, 2007) model across Moreton Bay (Fig. S1e). SWAN is a wave generation and propagation model, two-dimensional in the horizontal plane, which is used to convert wind measurements into spatial wave parameters (wave height $H_{RMS}$, mean wave period $T_m$ and peak wave energy direction $\theta_p$).

The model was generated using half hourly wind speed and direction from the Australian Government Bureau of Meteorology Station at Inner Beacon, from 2002 to 2010 (http://www.bom.gov.au/). The wave propagation model consisted of 10 grids (Fig. S2) and was calibrated using wave measurements from a buoy located at 27°15′S and 153°12′E (Fig. S2) between October 2000 and June 2010 operated by the Queensland Government (J. Waldron, unpublished data; Queensland Government Environmental Protection Agency, 2004).

*Rate of sea level rise.* Accelerating rates of SLR were simulated based on the Vermeer & Rahmstorf (2009) B1 scenario of 1.1 m by 2100. This scenario considers the melting of ice sheets and glaciers and assumes that there is some degree of mitigation of $CO_2$ emissions. The rate of SLR ($\dot{S}$) at year $Y$ increased linearly with time to according to the following:

$$\dot{S}(Y) = 0.1824Y - 362.89 \tag{3}$$

Eqn 3 predicts that $\dot{S}$ was 2 mm yr$^{-1}$ in 2000, which corresponds well to the observed rate of rise in the region of 2.4 mm yr$^{-1}$ between 2000 and 2010 (Lovelock *et al.*, 2011), and that it will be 20 mm yr$^{-1}$ in 2100. To examine the effect of magnitude of SLR on area of seagrass (see Analysis), the parameters of this equation were modified accordingly.

*Sediment accretion.* Net sediment accretion, defined as sediment accumulation minus subsidence and compaction, in seagrass habitats was parameterized at 2 mm yr$^{-1}$ based on a meta-analysis in C.M. Duarte, I.J. Losada, I. Hendriks, I. Mazarrasa & N. Marba, unpublished data. This value is similar to the net accretion observed in mangroves in Moreton Bay (Lovelock *et al.*, 2011). Sediment accretion is typically higher in vegetated than in unvegetated areas (Van Santen *et al.*, 2007); in the absence of local empirical data, net accretion data for non-seagrass habitats were assumed to be null. The model was subsequently used to explore the effect of accretion on area of seagrass (see Analysis and Fig. 6).

*Land cover data.* Suitability of substrate for seagrass in newly inundated areas was estimated by factoring in land cover maps obtained from Lyons *et al.* (2012). The extent of impervious surfaces at 30 m resolution was derived from a land cover map classified from a Landsat ETM + image for November 2009. Urban and developed land cover classes were classified as impervious areas, and all other land cover categories as potentially suitable for seagrass (Fig. S1f).

*Environmental conditions in newly inundated areas.* The marine environmental conditions in newly inundated areas due to SLR had to be estimated. New values for significant wave height were estimated by linearly interpolating from the nearest adjacent positions to the newly inundated regions. New values for Secchi depth were estimated at each time step using updated predictions of the linear model based on the maps distance to rivers, distance to open ocean and depth, which were updated based on the SLR conditions.

### *Model development, validation and implementation*

*Seagrass distribution model.* Species distribution models (SDMs), also known as niche or predictive habitat models, have emerged as a powerful tool for predicting the migration of organisms in response to climate change (Guisan & Zimmermann, 2000; Kearney & Porter, 2009; Wiens *et al.*, 2009; Robinson *et al.*, 2011). SDMs have been successfully used to relate seagrass presence or abundance to environmental variables (Fonseca & Bell, 1998; Lathrop *et al.*, 2001; Coles *et al.*, 2009; Grech & Coles, 2010), with the particular approach and variables used varying depending on spatial scale and relevant environmental drivers.

For this study, the presence vs. absence of seagrass was modelled by fitting a Generalized Linear Model assuming a binomial distribution to the input data, with the logarithm of % surface irradiance ('light'), significant wave height ('waves') and the interaction between light and waves, as predictor variables. While light may be influenced by waves due to the influence of sediment re-suspension on water clarity, over the scale of this study region light and waves are not directly related (Fig. S4). A spatial auto-correlation (SAC) term was not incorporated, since the purpose of the model was to simulate future conditions, whereby the assumption of the SAC term would be violated (A Guissan, *personal communication*). Model performance was assessed using a cross-validation procedure by splitting the data set of observations randomly into 75% for model fitting, and 25% for model evaluation (Grech & Coles, 2010; Chollett & Mumby, 2012) and repeating for 100 iterations. The procedure was repeated for 20 threshold values between 0 and 1 of probability of occurrence; for example, values above which seagrass is present, and otherwise is absent. Accuracy was assessed by 'sensitivity' (the percentage of correctly classified seagrass locations), 'specificity' (the percentage of correctly classified non-seagrass locations), false positives (the number of occurrences where the model predicts seagrass habitat in locations where is not observed) and false negatives (the number of occurrences where the model predicts non-seagrass habitat in locations where seagrass is observed) (Chollett & Mumby, 2012). The threshold cut-off value was selected as the value where sensitivity and specificity were both maximized.

A map of suitable seagrass habitat was generated using results of the habitat distribution model. For each grid cell, the probability of occurrence of seagrass ($p_i$) was calculated by applying an inverse logistic transformation:

$$p_i = \frac{e^{g(x_i)}}{1 + e^{g(x_i)}} \tag{4}$$

where $g(x_i)$ is the linear predictor fitted by the logistic regression. The model coefficients were used to calculate $g(x_i)$. Seagrass was classified as 'present' if probability of occurrence was greater than the threshold value.

*Sea level rise inundation model.* The simulated maps of seagrass distribution were used to initiate the SLR inundation model. The model was nominally initialized for the year 2000, as this was the closest decade to the 2004 seagrass maps used to create the model. The impact of SLR on depth was modelled by modifying the terrain model at 10 year time steps from 2000 to 2100 by incorporating SLR and sediment accretion by seagrass according to the following:

$$Z(x, y, t + \Delta t) = Z(x, y, t) - \int_t^{t+\Delta t} \dot{S}(\tau)d\tau + \dot{A}(i)\Delta t \tag{5}$$

where $z(x,y,t)$, m, is the depth at longitude $x$, latitude $y$ and time $t$, with negative values below mean sea level and positive values on land; $\dot{S}$ is the rate of SLR in mm yr$^{-1}$ at year $t$, and $\dot{A}$ is the accretion rate of sediment, which is a function of seagrass presence ($i = 1$; $\dot{A} = 2$ mm yr$^{-1}$) or absence ($i = 0$; $\dot{A} = 0$ mm yr$^{-1}$).

At each location in each time step, the presence/absence of seagrass was then re-estimated by applying the seagrass distribution model using the revised depth (Eqn 5) and the newly estimated environmental conditions. Seagrass habitat was only permitted to occur in areas connected to the contiguous ocean. If seagrass habitat was predicted in a grid cell containing an impervious surface it was prevented from establishing at that location. Otherwise, expansion of habitats into newly inundated regions was assumed to be complete and not limited by connectivity or existence of other ecosystems.

*Analysis.* At each time step, the following data were calculated: total area of potential seagrass habitat, area of potential habitat lost and area of potential habitat gained. The effect of impervious surfaces in newly inundated areas was examined by calculating the total area of seagrass habitat with and without the restriction of impervious surfaces preventing establishment. Data are presented as the percentage of area of suitable habitat occurring in 2100 compared to that available in 2000. Areas of relative loss, gain and no change in seagrass habitat between 2000 and 2100 were assessed for the entire bay, as well as for three subset regions occurring in the southern, eastern and western bay (indicated by white subset regions in Fig. 1). The median Secchi depth in each grid cell was related to whether the presence of seagrass habitat changed over time, and calculated for the particular subset regions.

In addition to the parameterization described previously, model runs were conducted between 2000 and 2100 using various combinations of the input parameters for magnitude of SLR (0.2–1.4 m), rate of sediment accretion in seagrass (0–10 mm yr$^{-1}$) and water clarity ($\pm$up to 50% of Secchi depth at each location). The results were used to calculate the increase in water clarity or accretion rate in seagrass required to offset particular magnitudes of SLR.

## Results

### *Seagrass distribution model*

The probability of seagrass presence increased with higher light penetration, decreased with greater wave height, and there was a significant interactive effect of light $\times$ waves (Table S2). The binomial model of seagrass presence vs. absence in relation to $\log_{10}$% irradiance and significant wave height ($H_s$, m) explained 39.7% of the null deviance, and the linear predictor took the form:

$$\begin{aligned} g(x_i) = -1.03 + 0.65\left(log_{10}\frac{I(Z)}{I_0}\right) - 7.13(H_s) \\ + 4.43(H_s \times log_{10}\frac{I(Z)}{I_0}) \end{aligned} \tag{6}$$

The modelled probability of seagrass presence fit the observations very closely at all light levels (Fig. 3a). At low light levels, the probability of occurrence for seagrass was greater for low wave heights, whereas in high light the probability of occurrence for seagrass was greater for higher wave heights (Fig. 3a).

From the validation procedure, a threshold probability of occurrence of 0.16 was selected as a cut-off to determine seagrass presence and absence (Fig. 3b). This threshold maximized sensitivity and specificity, resulting in seagrass habitat and non-habitat being correctly classified in 83% of cases (Table S4). The rate of false positives for seagrass presence was higher than that of false negatives (62% vs. 3%, Table S4). This is because

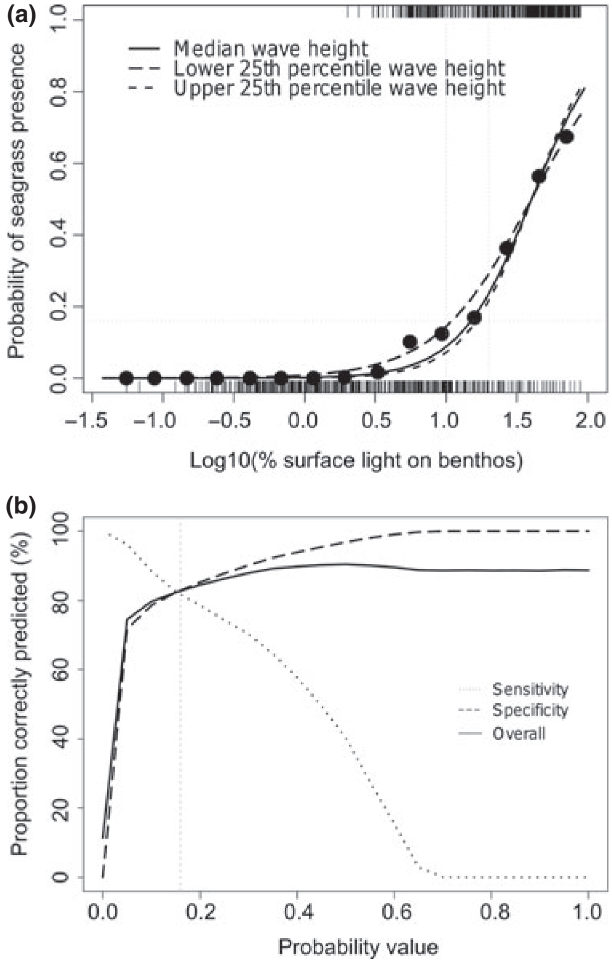


**Fig. 3** Logistic regression model used to classify seagrass habitat in Moreton Bay, Southeast Queensland, Australia. (a) Predicted probability of seagrass presence as a function of the logarithm of the % surface irradiance. Continuous lines indicate the fitted model for 3 categories of significant wave height. Dashed lines on the upper and lower x-axis represent observations of seagrass presence (1) and absence (0) at given light levels, respectively. Circles indicate the average and standard error of presence vs. absence data for 15 categories of light (pooled across wave heights). The dashed horizontal line indicates the threshold value (0.16) selected during the validation procedure (See b), where values above and below the threshold are categorized as seagrass presence and absence, respectively. Vertical grey dashed lines indicate 10% and 20% light (1 and 1.3 log scale), corresponding to the published minimum light tolerance of seagrass. (b) Model sensitivity (% seagrass habitat correctly classified), specificity (% non-seagrass habitat correctly specified) and overall (% seagrass and non-seagrass habitat correctly specified). The horizontal grey dashed line indicates the optimal threshold value (0.16).

there are approximately 10 × more locations where seagrass is absent than where it is present, and therefore reducing the rate of false negatives has a relatively greater effect on maximizing model sensitivity and specificity, which are by definition standardized by sample size. The total area of potential seagrass habitat predicted for 2000 was 346 $km^2$, almost double compared to the area of seagrass mapped in 2004 [189 $km^2$, (Roelfsema *et al.*, 2009)]. The threshold cut-off value intersected with the modelled probability of seagrass occurrence at $log_{10}$% light of approximately 1–1.25, corresponding to % light levels of ~10–18% (Fig. 3a).

The model captures the overall spatial patterns in seagrass habitat distribution in Moreton Bay described by Roelfsema *et al.* (2009) (Fig. 4a), with extensive habitat area predicted in the Eastern Banks, and smaller areas predicted in the southern, western and northern portions of the bay (Fig. 4b, Fig. 4c). Areas of absence were predicted in deeper, more turbid and more wave-exposed locations. The modelled false positives tended to occur in areas of deeper and/or more turbid water, particularly in Bramble and Deception Bay (Fig. 4d).

*Effect of SLR on temporal and spatial patterns in distribution.* A landward shift in the distribution of seagrass habitat in Moreton Bay is predicted in response to 1.1 m SLR by 2100 (Fig. 5a). Loss occurred at the deeper edge of the seagrass extent, whereas new habitat was created in newly inundated regions containing suitable substrate. The proportion of locations where habitat remained suitable for seagrass varied spatially within the modelled area (Fig. 5a, Fig. S5). In the southern bay, 19% of existing seagrass habitat was lost by 2100, compared to the eastern bay where loss of only 5% occurred (Fig. S5). The percentage of existing habitat predicted to be lost by 2100 was highest in the western bay (41%). Relative area gained was 2%, 3% and 6% in the southern, eastern and western portions of the bay, respectively. In all regions, a smaller percentage of seagrass habitat was gained than was lost, leading to an overall decline in the area of seagrass habitat. Overall, the Eastern Banks were the area least affected by SLR.

*Impervious surfaces.* With 1.1 m of SLR, the total area of potential seagrass habitat declined non-linearly through time from 346 $km^2$ to 288 $km^2$ from 2000 to 2100, corresponding to overall loss of 17% (Fig. 5b). This is a conservative estimate of loss since development in the coastal zone is likely to continue over the next century further removing potential habitat. The trajectory of loss through time was strongly affected by the criteria for migration of seagrass into newly inundated areas. Considering a management scenario where impervious surfaces are removed in inundated areas, the area of seagrass in 2100 declined by only 5% relative to 2000. In this scenario, the minimal extent of seagrass occurred in 2090, after which it increased. This result is

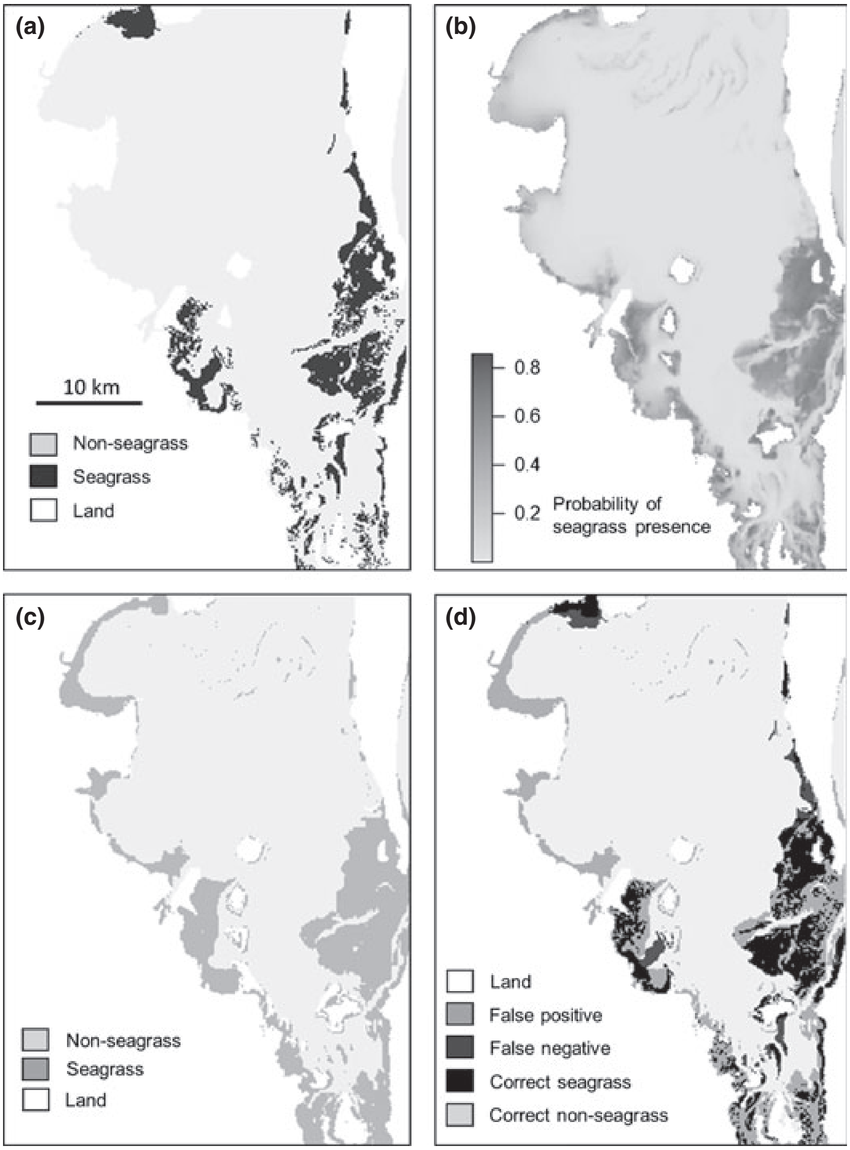


**Fig. 4** Comparison of observed and modelled probability of seagrass presence vs. absence in Moreton Bay, Southeast Queensland, Australia, in 2000. (a) maps of seagrass observations from Roelfsema *et al.* (2009); (b) modelled probability of seagrass presence; (c) Map of seagrass presence vs. absence, derived from (b) and based on a threshold cut-off probability of presence of 0.16 selected during the validation procedure; (d) Map indicating spatial variability in correct classification, false positives (locations where the model predicts seagrass but where there was none observed), and false negatives (locations where seagrass is observed but was not predicted to occur by the model).

an effect of shoreline geometry and coastal topography, where once sea level reaches above a particular height, the slope of the shoreline is less and larger areas become inundated.

*Water clarity.* Median Secchi depth was approximately 1 m less in areas where seagrass loss was predicted (2 m), compared to areas where no change in seagrass distribution (3 m) was predicted due to SLR (Fig. S6). Median Secchi depth in areas of predicted seagrass habitat gain was similar to areas of loss, but the processes influencing addition of habitat will be more strongly influenced by topography than by water clarity. The percentage of existing habitat available in 2100 varied non-linearly with magnitude of SLR and water clarity (Fig. 6a). Reductions in water clarity increased the area of seagrass affected by a particular magnitude of SLR. Conversely, improvements in water clarity of

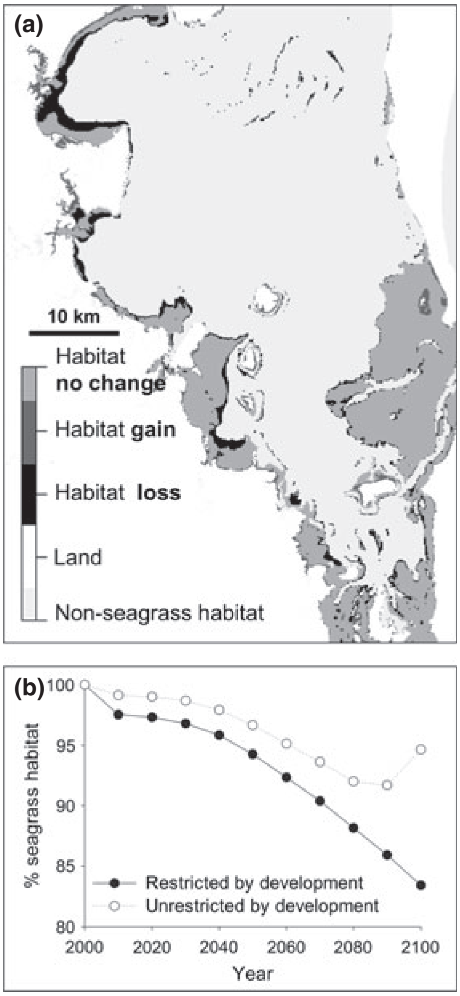


**Fig. 5** Effect of predicted 1.1 m sea level rise by 2100 on distribution and abundance of seagrass in Moreton Bay, Southeast Queensland, Australia. (a) Change in distribution of seagrass suitable habitat, indicating areas of seagrass habitat present in 2000 at risk of loss by 2100, new habitat gained in 2100, and areas of no change between 2000 and 2100. (b) Percentage of seagrass habitat in 2100 relative to 2000. Seagrass loss is predicted to be higher if establishment in newly inundated areas is restricted by existing coastal development. The upturn in relative area after 2090 in the unrestricted scenario is caused by shoreline geometry, where a threshold sea level height is reached and then inundation of landward areas increases.

approximately 30% could potentially offset anticipated losses of seagrass habitat due to 1.1 m SLR, with greater magnitudes of SLR requiring larger improvements in water quality.

*Sediment accretion.* The rate of sediment accretion affected the percentage of suitable habitat non-uniformly under a range of SLR estimates (Fig. 6b). For magnitudes of SLR 80 cm or greater, and for rates of sediment accretion <4 mm yr$^{-1}$, the area of seagrass was positively related to rate of sediment accretion (Fig. 6b). For SLR less than 80 cm, and for rates of sediment accretion >4 mm yr$^{-1}$, the percentage of habitat was highest for SLR around 20–80 cm. If the rate of sedimentation is higher than the average rate of SLR, seagrass habitats will gradually emerge and become non-viable, and thus there will be a reduction in total area. For a given magnitude of SLR, there was ~2% increase in area of seagrass for an increase in sediment accretion of 1 mm yr$^{-1}$.

## Discussion

Predicted sea level rise due to climate change will likely cause a decrease in the abundance of seagrass in Moreton Bay, Australia, over the coming century. For SLR of 1.1 m in conjunction with the existing extent of coastal development, seagrass habitat area was predicted to decline by 17% from 2000 to 2100. Management to improve water quality and facilitate shoreward migration of ecosystems will increase the likelihood that coastal ecosystems will persist under SLR.

### *SLR and water quality*

In this study, losses of seagrass habitat were highest in the western bay where water clarity was lowest. Losses of seagrass globally over recent decades have been primarily due to reduced water quality and clarity (Waycott *et al*., 2009; Short *et al*., 2011), and deepening water due to SLR will exacerbate the effects of this stressor. Management efforts to improve water quality will have multiple benefits – both by improving present conditions (Santos & Lirman, 2012), and improving the future response of seagrass to SLR.

There may be an opportunity to offset potential losses of seagrass due to SLR by improving water quality. We found that the impact of 1.1 m of SLR could be offset by increasing average Secchi depth by approximately 30%. Otherwise stated, management actions to reduce nutrient and suspended sediment loads in coastal waterways could potentially offset the impact of predicted SLR. Over the past decade, Southeast Queensland has invested $300 million on sewage treatment plant upgrades, and $2.5 million on the restoration of riparian areas (EHMP, www.ehmp.org). These efforts have had a positive effect on water quality in Moreton Bay (Saeck *et al*., in press). Water clarity varies over multiple spatial and temporal scales, and further research on the seasonality in water quality effects on seagrass, as well as its interaction with other stressors, such as temperature, is recommended.

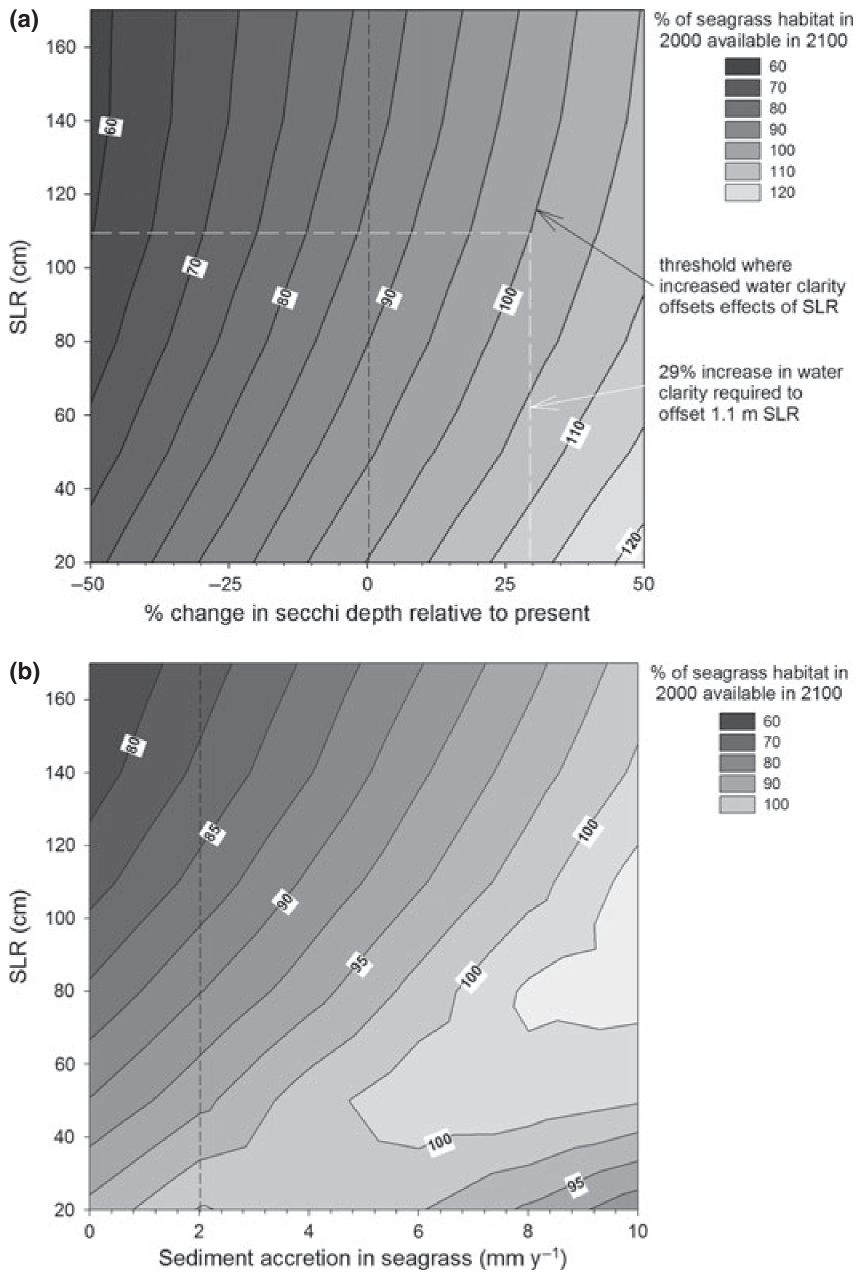


**Fig. 6** Effects of magnitude of sea level rise (SLR), water clarity, and sediment accretion rate on the area of seagrass habitat in Moreton Bay, Southeast Queensland, Australia, as a % of the habitat available in 2000. (a) Varying SLR and Secchi depth for a constant accretion rate of 2 mm $yr^{-1}$. Secchi depth varies spatially in the study area and was modified by changing the intercept of the model used to estimate Secchi depth as a function of distance to rivers, the open ocean, and depth by up to ±50%. Dashed line indicates the baseline Secchi depth values. (b) Varying SLR and sediment accretion rate in seagrass for the normal water clarity conditions in the bay (see Methods). Dashed line indicates accretion rate of 2 mm $yr^{-1}$ which was used for all other analyses.

*Coastal squeeze*

The presence of impervious surfaces will prevent the inland migration of coastal ecosystems, such as seagrass (*this study*) and saltmarsh (Schmidt *et al.*, 2012) which will decrease habitat availability for threatened wildlife (Traill *et al.*, 2011; Schmidt *et al.*, 2012). Impacts could be mitigated by ensuring suitable substrate is available in newly inundated regions. This would require preventing or removing armouring of coastlines, and removing impervious surfaces in the coastal zone as the sea rises (Abel *et al.*, 2011). This scenario is less likely to occur in highly developed coastal areas with valuable assets where people will tend to defend shorelines in response to rising seas (Nicholls, 2011), but it may be a more feasible conservation option in sparsely populated areas where the cost of defence on a per capita basis will be relatively high.

This model assumes that seagrass may colonize any suitable newly inundated area. In reality, the process of seagrass colonization is complex, and there will be a time delay of up to many decades before seagrass will become established (Meehan & West, 2000). Seagrass colonization occurs either by extension of vegetative rhizomes and/or by recruitment of seedlings (Kendrick *et al.*, 1999), and tends to occur more rapidly if seed banks are present in the sediments (Marbà & Duarte, 1995). However, seed banks are unlikely to be present in areas newly inundated by SLR. Therefore, colonization will depend on the proximity of source populations for either vegetative expansion or dispersal of seeds. Studies of seagrass loss and recovery suggest there will be considerable uncertainty in rates of colonization, since unvegetated sediments tend to be unstable, promoting re-suspension of sediments, and reducing water clarity (Gacia & Duarte, 2001; Van Der Heide *et al.*, 2007; Carr *et al.*, 2010). Interesting community dynamics may occur if seagrass expansion is prevented by the persistence of upland coastal vegetation such as mangroves within the low intertidal zones. Further research on the processes affecting establishment of seagrass in the context of SLR is required.

### *Influence of sediment accretion*

Seagrass response to SLR will depend on the relative rates of sedimentary accretion vs. SLR. If the rate of accretion is similar to the rate of SLR, then existing seagrass habitat will be less prone to loss, and the area of seagrass may expand as seagrass establishes in newly inundated areas (e.g. Kairis & Rybczyk, 2010). However, rapid sediment accretion could facilitate the transition of seagrass into mangrove or marsh habitats. On the other hand, if rates of accretion are much lower than rates of SLR then the deep edge of seagrass habitats will be lost as conditions become unsuitable, as was found in this study. In general, as rates of SLR increase the persistence of these important habitats will become increasingly reliant on migration.

Unfortunately, long-term rates of accretion in seagrass have not been well characterized. A recent meta-analysis (C.M. Duarte, I.J. Losada, I. Hendriks, I. Mazarrasa & N. Marba, unpublished data) found an average accretion rate of 2 mm yr$^{-1}$ from eight studies dating sediment cores, which was used to parameterize the present model. In reality, rates of sediment accretion in seagrass vary spatially and temporally (Bos *et al.*, 2007), may vary with depth, and may respond to SLR, as is observed in other coastal ecosystems (Morris *et al.*, 2002). As an added complexity, the cause of increased rates of sediment accretion in seagrass could be increased concentrations of suspended sediments, which in turn would diminish benthic light availability. This would cause a change in shoot morphology (Abal *et al.*, 1994; Longstaff *et al.*, 1999) potentially reducing the capacity of seagrass to entrain particles (Gacia *et al.*, 1999). Future research examining the biological and environmental processes influencing sediment accretion in seagrass is recommended.

### *Performance of statistical distribution model*

Seagrass habitat or non-habitat could be successfully predicted in 83% of cases. The threshold cut-off value of 0.16 selected in the optimization procedure corresponded to seagrass being classified as present if it occurred in regions with % irradiance greater than 10–18%, depending on wave height. This is in close agreement with reviews of the average minimum light requirement for seagrass of approximately 10% (Dennison, 1987; Duarte, 1991).

The error rate for false negatives (3%) was much lower than for false positives (62%). This suggests that light and wave conditions confer necessary conditions for the presence of seagrass in Moreton Bay but that all 'suitable' habitat is not filled for unidentified biological or physical factors. Historical loss and lack of recovery by seagrass, or the presence of other species such as the green algae *Caulerpa* (Burfeind & Udy, 2009), are likely to influence seagrass presence at a given area. For instance, seagrass habitat was predicted in the southern section of Deception Bay and in Bramble Bay, both areas where historical loss of seagrass has occurred (Hyland *et al.*, 1989; Dennison & Abal, 1999). Recovery of seagrass in areas of loss does not always occur due to feedbacks between suspended sediments, water clarity and seagrass density (Carr *et al.*, 2010, 2012a,b). The model also predicted seagrass in many of deeper the channels of the Eastern Banks; these areas were mapped with less accuracy than the shallower areas (Roelfsema *et al.*, 2009), and therefore the modelled false positive errors may actually reflect false negative errors in the mapped seagrass data. Despite recognized limitations in the seagrass habitat input data, this study incorporated data obtained using state of the art, and therefore 'best available', coastal habitat mapping techniques. Mapping deep seagrass is known to be problematic, and habitat distribution models can inform such research (e.g. Coles *et al.*, 2009).

### *Assumptions, uncertainty and limitations*

Combining multiple data sets and products into a model required numerous assumptions and generates associated uncertainty. Details for the accuracy of each data source can be found in Table 1. The seagrass data were derived from a variety of sources, including remote sensing, and as a consequence, some deep seagrass habitats were not represented in the input data set. Deep seagrass habitats will be the most threatened by SLR, and hence the rates of seagrass loss predicted in this study will likely underestimate the area of seagrass that will be under threat. Accuracy in the underlying terrain model will affect results of SLR models (Runting *et al*., 2012). We used the best available terrain model, although most certainly improvements in data quality and resolution, particularly in the nearshore zone, would increase the accuracy of results.

The study system was modelled using static representations of environmental parameters. In reality, light availability to the benthos is not uniform, but is influenced by seasons, climate and extreme events such as floods and storms. However, in Moreton Bay, use of mean benthic irradiance was a very good approximation to higher temporal resolution light data for predicting seagrass presence (O'Brien *et al*., 2011).

Large-scale geomorphological changes, such as migration or opening of channels, may occur in the case of rapid SLR (Ranasinghe *et al*., 2012), but were considered beyond the scope of this study. Likewise, shoreline erosion was not explicitly considered in the model. According to the Bruun Rule (Bruun, 1962), on high energy sandy shores 100 m recession of the coastline would be expected for 1 m SLR. However, those conditions do not occur within the study area. Moreover, the spatial extent of erosion would affect only one grid cell in width at shore, and therefore incremental changes in the shoreline profile could not be simulated. This quantity of erosion was considered to be relatively minor given the scale of the seagrass meadows in the eastern bay (kms wide). In the western bay, of 13.1 $km^2$ of potential erodible area, 79% were impervious surfaces (J. Leon, unpublished data), and may be assumed to be defended against inundation and erosion.

Sea level rise, urbanization and poor water quality are but a component of a suite of pressures that will affect seagrass over the coming century. Other symptoms of climate change, such as warming temperatures, increased intensity of cyclones and altered patterns of precipitation, including extreme floods, are also predicted to have a detrimental effect on seagrasses (Short *et al*., 1999; Campbell & Mckenzie, 2004; Campbell *et al*., 2006; Duarte, 2002; Collier *et al*., 2011; Rasheed & Unsworth, 2011), but were deemed beyond the scope of this study. Further research into the effects of multiple stressors will facilitate the development of increasingly realistic models of future seagrass populations required to inform management.

### *Management implications and future research*

Rapid sea level rise will provide an additional stressor to valuable yet threatened seagrass ecosystems. In Moreton Bay, Southeast Queensland, Australia, a decline of 17% in overall area of seagrass habitat is anticipated based on sea level rise of 1.1 m by 2100 and the presence of existing development which will prevent the inland migration. Future research to disentangle the effects of suspended sediment on accretion and benthic light availability will improve models of the effects of SLR on seagrass. Management efforts to maintain or improve water clarity will promote the persistence of seagrass at the deep edge of the extent as sea level rises. Allowing space for seagrass and other wetland ecosystems in coastal areas will facilitate migration into newly inundated areas.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Data used to model seagrass presence vs. absence in Moreton Bay, Southeast Queensland, Australia.
**Figure S2.** Wave propagation model (SWAN) layout, consisting of ten grids (model grids 0–9).
**Figure S3.** Significant wave height comparisons between measurements and prediction.
**Figure S4.** Relationship between $\log_{10}$(% benthic irradiance) to significant wave height (m) in Moreton Bay, Australia.
**Figure S5.** Change in distribution of seagrass suitable habitat in Moreton Bay, Southeast Queensland, as a result of sea level rise of 1.1 m.
**Figure S6.** Variation in Secchi depth in areas of predicted seagrass habitat loss, gain, and no change in 2100 compared to 2000 due to 1.1 m sea level rise in Moreton Bay, Southeast Queensland, Australia.
**Table S1.** Results of linear model used to relate field measurements of Secchi depth (m) to the Euclidean distance to rivers (m), distance to open ocean (m) and to water depth (m).
**Table S2**. Grid resolution and rotation.
**Table S3.** Regression coefficients, standard errors, $t$ and $P$ values for the logistic regression model predicting seagrass presence in Moreton Bay, SE Queensland, Australia.
**Table S4.** Error matrix for the observed and predicted presence and absence of seagrass in Moreton Bay, Southeast Queensland, using a threshold cut-off value of 0.16 to classify presence vs. absence based on probability of occurrence.