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Interdependency of tropical marine ecosystems in response to climate change

Megan I. Saunders
University of Queensland

Javier X. Leon
University of Queensland

David P. Callaghan
University of Queensland

Chris M. Roelfsema
University of Queensland

Sarah Hamylton
University of Wollongong, shamylto@uow.edu.au

See next page for additional authors

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Abstract

Ecosystems are linked within landscapes by the physical and biological processes they mediate. In such connected landscapes, the response of one ecosystem to climate change could have profound consequences for neighbouring systems. Here, we report the first quantitative predictions of interdependencies between ecosystems in response to climate change. In shallow tropical marine ecosystems, coral reefs shelter lagoons from incoming waves, allowing seagrass meadows to thrive. Deepening water over coral reefs from sea-level rise results in larger, more energetic waves traversing the reef into the lagoon1, 2, potentially generating hostile conditions for seagrass. However, growth of coral reef such that the relative water depth is maintained could mitigate negative effects of sea-level rise on seagrass. Parameterizing physical and biological models for Lizard Island, Great Barrier Reef, Australia, we find negative effects of sea-level rise on seagrass before the middle of this century given reasonable rates of reef growth. Rates of vertical carbonate accretion typical of modern reef flats (up to 3 mm yr−1) will probably be insufficient to maintain suitable conditions for reef lagoon seagrass under moderate to high greenhouse gas emissions scenarios by 2100. Accounting for interdependencies in ecosystem responses to climate change is challenging, but failure to do so results in inaccurate predictions of habitat extent in the future.

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Authors

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Authors:

Megan I. Saunders[1,2], Javier X. Leon[1,3], David P. Callaghan[4], Chris M. Roelfsema[3], Sarah Hamylton[5], Christopher J. Brown[1,2], Tom Baldock[4], Aliasghar Golshani[4], Stuart R. Phinn[1,3], Catherine E. Lovelock[1,6], Ove Hoegh-Guldberg[1], Colin D. Woodroffe[5], Peter J. Mumby[1,2]

Author Affiliations:

1 The Global Change Institute, The University of Queensland, St Lucia Qld 4072, Australia
2 Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia Qld 4072, Australia
3 School of Geography, Planning and Environmental Management, University of Queensland, St Lucia Qld 4072, Australia
4 School of Civil Engineering, The University of Queensland, St Lucia Qld 4072, Australia
5 School of Earth and Environmental Sciences, University of Wollongong, Wollongong, NSW 2522, Australia
6 The School of Biological Sciences, The University of Queensland, St Lucia Qld 4072, Australia

Corresponding Author Address:

m.saunders1@uq.edu.au

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Ecosystems are linked within landscapes by the physical and biological processes they mediate. In such connected landscapes, the response of one ecosystem to climate change could have profound consequences for neighbouring systems. Here, we report the first predictions of interdependencies between ecosystems in response to climate change. In shallow tropical marine ecosystems, coral reefs shelter lagoons from incoming waves allowing seagrass meadows to thrive. Deepening water over coral reefs from sea-level rise results in larger, more energetic waves traversing the reef into the lagoon[1,2], potentially generating hostile conditions for seagrass. However, coral reef growth to maintain relative water depth could mitigate negative effects of sea-level rise on seagrass. Parameterising physical and biological models for Lizard Island, Great Barrier Reef (Australia), we find negative effects of sea-level rise on seagrass before mid-century given reasonable rates of reef growth. Rates of carbonate accretion typical of modern reef flats (up to 3 mm yr^{-1}) will likely be insufficient to maintain suitable conditions for reef seagrass under moderate to high greenhouse gas emissions scenarios by 2100. Accounting for interdependencies in ecosystem response to climate change is challenging, but failure to do so results in inaccurate predictions of habitat extent in the future.

Climate change affects the distribution, extent and functioning of ecosystems[3]. Ecosystems comprise living organisms and the nonliving components of their environment in an interacting system. Interactions between distinct ecosystems also occur– for instance, where one ecosystem modifies adjacent environments, allowing other ecosystems to thrive where they otherwise would not exist. At the species level, interdependencies in response to climate change occur when interacting species have different responses to a climate stressor[4]. This can alter interactions such as competition, rates of pathogen infection, herbivory and predation[5,6]. We propose that interdependencies in response to climate change at the ecosystem level could also exist, but these have not previously been documented.

In shallow tropical seas, coral and seagrass exist in a patchy habitat mosaic, connected by numerous biological, physical and-chemical linkages[7,8]. Seagrass supports early life-stages of many reef fish[7]; provides a buffer against low pH[8]; binds sediments to reduce erosion[9] and filters nutrients and sediments from water[9,10]. In turn, the distribution of shallow seagrass meadows which thrive in low energy wave environments[9] depends on wave sheltering by coral reefs. Seagrass and coral reefs support the livelihoods of many of the 1.3 billion people who live within 100 km of tropical coasts[11]. Unfortunately, rapid and widespread declines of these habitats are occurring worldwide[12,13]. Accurately predicting effects of climate change on tropical marine ecosystems is essential for developing appropriate management plans to maintain human well-being.

Sea-level rise (SLR) drives changes in the distribution of seagrass[14] and coral reefs[15]. Despite considerable uncertainty, SLR of up to 1 m by 2100 may occur given business as usual greenhouse gas emissions scenarios[16,17,18]. Rising seas can result in inland migration of coastal habitats, loss of habitat at the seaward edge, vertical accretion to maintain relative position with sea level, adaptation to new conditions, or a combination thereof[14]. Coral reef growth (carbonate accretion) occurs by calcification of corals and coralline algae, and subsequent in-filling of the reef matrix[19,20]. Sediment accretion in seagrass meadows occurs by the production of roots and rhizomes, and by promotion of high rates of sediment deposition and retention[9].

Our aim was to predict the response of seagrass distribution to altered wave conditions resulting from rising seas and the response of distinct ecosystems (coral reefs and seagrass) to changes in sea level [Fig 1]. We examined this process at an intensively studied coral reef environment at Lizard Island, Great Barrier Reef [Fig. 2A], where there is a gradient of wave exposure over shallow water habitats[15,21,22].

The first task was to understand the relationship between the wave environment and the distribution of seagrass. To do so, we built a Species Distribution Model (SDM)[23] of shallow water (< 5 m) seagrass habitats as a function of the wave environment. Field data on water depth[21] [Fig. 2B] and distribution of benthic habitats [Fig. 2C] were collected and mapped to 5x5 m resolution using remote sensing techniques. Synoptic maps of parameters characterising the wave environment (benthic root mean square wave orbital velocities (m s^{-1}, hereafter U_{RMS}), peak wave periods (s, hereafter T_p), and significant wave heights (m, hereafter H_s)) [Fig 2 D-F] at the same locations were generated using bathymetry and wind data as input to the Simulating WAves Nearshore (SWAN)[24] model. Spatial auto-correlation (SAC) was removed following the residual autocorrelate (RAC) approach[25].

SAC may represent un-modelled environmental variables or population processes such as dispersal, and it is debated whether it should be accounted for in SDMs used to predict future scenarios[26,26]. Therefore, predictions of future seagrass distribution (see Figs. 3, 4) are presented for 2 scenarios[27]: 1) current spatial dependencies, such as limits to colonisation, persist into the future ("spatial model"); and 2) present and future distribution of seagrass is not limited by current spatial dependencies ("non-spatial model"). The non-spatial model makes less accurate predictions of present day distribution, but may more accurately predict seagrass redistribution in the future. This may be more realistic than scenario 1, as the size of the study area is small, thus seagrass is unlikely to be limited by dispersal over multiple decades.

Seagrass presence vs. absence was correctly classified by the spatial model in 99.5 ±0.03 % of cases (deviance explained = 90%; $p < 0.01$). The probability of seagrass presence declined with increases in each of the wave parameters (H_s, T_p, and U_{RMS}) [Fig. S3-2]. Increases in erosion, plant breakage, reductions in establishment potential, or a combination of factors may drive this relationship.

The next step was to examine how deeper water resulting from SLR, in the absence of accretion in either habitat, would affect the distribution of seagrass. To do so, we simulated SLR of 1 m by increasing water depth at all locations, re-calculated the wave parameters using SWAN, and predicted seagrass distribution using the SDM based on the revised wave parameters. Using the spatial model, SLR of 1 m reduced the area of habitat suitable for seagrass by 10%, from 6.5 to 5.7 hectares [Fig. 3]. Losses were due to larger, more energetic waves crossing the reef crest, resulting in increases in the magnitude of U_{RMS}, T_p, and H_s in the lagoon. The non-spatial model, in which spatial dependencies in habitat occurrence were omitted, predicted 85% seagrass habitat loss from 1m SLR [Fig. 3].

In reality, bathymetry will be modified by geomorphic and ecological feedbacks during SLR such as sediment accretion and reef growth. To examine the effect of ecosystem specific response to SLR on the likelihood of seagrass occurring, we factored in habitat specific accretion to modify the bathymetry concurrently with SLR.

From this point onwards, for computational efficiency, we used only a subset of data occurring along a 1 dimensional (1D) transect passing over the reef and through the seagrass [Fig. 2A]. Two sets of scenarios were examined: 1) the coral reef platform, and/or the inner lagoon, could accrete to 1 m (or not) by 2100 to keep pace with 1 m SLR; and 2) SLR magnitudes ranging from 45-135 cm by 2100, corresponding to published SLR trajectories[16,17], and rates of reef growth ranging from 1-10 mm yr^{-1} [20], were considered at 4 points in time (2030, 2050, 2080, and 2100). Using these revised bathymetries we calculated the wave parameters using SWAN, and predicted the likelihood of seagrass occurring using the SDM.

For both the spatial and non-spatial models, the area of habitat on the transect suitable for seagrass depended on whether reef growth occurred in response to SLR, and was less affected by sediment accretion in seagrass [Fig. 4]. When both habitats "kept pace" with SLR, the area of seagrass in 2100 did not change compared to present. When neither sediment accretion nor reef growth, or only sediment accretion in seagrass occurred, all seagrass suitable habitat was lost, because T_p, H_s and U_{RMS} increased in the lagoon. When only reef growth occurred, seagrass habitat remained suitable, but declined to ~20% relative to present. Together, this suggests that seagrass will be strongly affected by altered wave environments resulting from changing water depth.

The likelihood of seagrass suitable habitat occurring along the transect at particular points in time decreased with increasing magnitude of SLR, and increased with increasing magnitudes of reef growth [Fig. 5]. For concision we show only results of the spatial model, since trends did not vary between different representations of the 1D model [e.g. Fig. 4]. For a given scenario of reef accretion and SLR, the area of seagrass suitable habitat declined through time. Impacts on seagrass begin to be evident as early as 2030, where rates of accretion <5 mm yr^{-1} result in hydrodynamic conditions less suitable for seagrass for all emissions trajectories. This surprising finding was driven by non-linearities in seagrass response to increased wave height, period and orbital velocity, whereby threshold conditions in wave disturbance were surpassed. By 2050, rates of accretion of at least 3 mm yr^{-1} are required to maintain suitable conditions for seagrass for the most conservative SLR trajectory, and rates of accretion of > 4.5 mm yr^{-1} are required to maintain the extent of seagrass habitat that is observed at present. By 2080 and 2100, conditions for seagrass become unsuitable except for under the most conservative SLR trajectory and for rates of reef accretion > 4 mm yr^{-1}. By 2100, habitat is unsuitable for seagrass, for all rates of coral accretion examined, for SLR of ~1 m or greater.

Healthy coral reef flats accrete at a maximum rate of ~3 mm yr^{-1}; higher rates tend only to be observed on productive reef slopes[15,20]. Our results suggest that reef growth of 3 mm yr^{-1} will facilitate seagrass habitat suitability until 2050 under moderate greenhouse gas emissions scenarios (e.g. RCP 4.5), but will not support seagrass habitat for higher SLR trajectories or at later points in time. Degraded reef environments accrete more slowly or may even erode[19,28], contributing additional relative SLR. The multiple stressors affecting reefs, including overfishing, coastal development, pollution, disease, warming temperatures and acidification[13] reduce carbonate budgets and therefore diminish capacity of reefs to accrete in response to rising seas[19,28]. Here we have identified that negative impacts on reefs may also be felt indirectly in adjacent seagrass habitats.

Our study shows that seagrass distribution depends on wave conditions, which in reef-lagoonal systems are mediated by the depth of the surrounding reef[1,2,29]. Maintaining net accretion capacity of reefs through mitigation of regional stressors (e.g. fishing regulations)[28] will therefore benefit adjacent seagrass meadows subject to SLR. This will be required for the continued provision of ecosystem services provided by seagrass, such as nursery areas, grazing grounds, and carbon sequestration[10]. Conversely, loss of seagrass could also have further negative consequences for coral reefs, due to decreased availability of nursery habitats, increased turbidity, or reduced pH[7-9].

There are several caveats to this research. Only seagrass occurring in 0-5 m depth was modelled, which may result in a conservative estimate of loss, because deep seagrass will be negatively affected by reduced light from deepening water[14]. While the effects of warming and acidification on reefs were accounted for implicitly by considering scenarios with low accretion rates, their effects on seagrass were not explicitly considered. This could be addressed through developing mechanistic models for seagrass dynamics, which could additionally consider shoreline erosion and sediment transport. This would overcome limitations of statistical models, which have a number of key assumptions[23]. To date, such models for seagrass have typically been limited to single locations[e.g.30].

Predicting the redistribution of ecosystems in response to climate change is significantly more complex than modelling the responses of individual ecosystems. Intricate dependencies may be disrupted by rapid climate change, and should ideally be considered in predictive ecological models. Failure to account for interdependencies in ecosystem response to climate change results in inaccurate predictions of future habitat extent. Both reductions in greenhouse gas emissions and effective local scale management across multiple habitats will likely be required to prevent the unravelling of interdependencies between ecosystems.

Methods

Study site. Lizard Island (14.7° S, 145.5° E) is a granitic island located 30 km off the coastline of Northern Queensland, Australia [Fig . 2]. A barrier reef encloses a 10 m deep lagoon, inshore of which patch reefs and seagrass meadows comprised primarily of *Thalassia hemprichii*, *Halodule uninervis*, and *Halophila ovalis* occur. The climate is tropical, with winds predominantly from the southeast. Long period swells are dissipated by the outer Great Barrier Reef. Tides are semi-diurnal, with a maximum range of 3 m.

Modelling overview. A habitat distribution model for presence vs. absence of seagrass in 0-5 m depth was developed based on U_{RMS}, T_p, and H_s. A graphical overview of the approach is available in Fig. S3-1.

The model was first developed and implemented using 2D spatial data at 5x5 m resolution for the entire study area. Wave conditions in 2100 based on 1 m SLR without any reef growth or sediment accretion were then simulated and used to predict occurrence of seagrass in the future in absence of geomorphic response to SLR.

For computational efficiency, subsequent analyses used data along a 1D transect sampled at 1 m resolution traversing the reef crest and through the seagrass towards shore [Fig. 2a]. The effect of varying magnitudes of seagrass sediment and reef accretion on hydrodynamic conditions were calculated using SWAN. Resultant wave parameters were used to calculate probability of seagrass habitat occurring in the future under various scenarios.

The total area examined was 39.6 km^2 (1,585,142 cells of 5x5 m); of this, 6.1 km^2 (244,000 cells) were between 0-5 m depth and used to model the 2D scenario. The 1D transect was 2173 m long and sampled every 1 m; 1812 cells of 1 m were between 0-5 m depth. Data layers were collated using ESRI ArcMap™ 10.0 and exported to RStudio v.0.98.501 for analyses.

Input data. Spatial data were based on a Worldview 2 satellite image (2x2m pixel size) captured in October 2011, and field data collected in December 2011 and October 2012. A Digital Elevation Model (DEM) was derived using multiple data sources[21]. Habitat data were collected using geo-referenced photo transects at 1-5 m depth by snorkel and SCUBA. Photos were analysed for benthic habitat and substrate composition. A map of benthic habitats was generated using Object-Based Image Analysis with the field data for calibration and validation [Supplemental 1].

Wave modelling. Synoptic maps of wave parameters were created using The Simulating WAves Nearshore (SWAN) model across Lizard Island[29]. The model was generated using half-hourly wind speed and direction from the Australian Government Bureau of Meteorology Station at Cape Flattery from 1999 to 2009. For each location 6 wave parameters were derived: mean and 90th percentile over 10 years of significant wave height (H_s), peak period (T_p), and benthic wave orbital velocity (U_{RMS}), respectively [Supplemental 2].

Species distribution model (SDM). SDMs for seagrass presence vs. absence were developed using wave parameters as predictor variables. Separate models were built for 2D and 1D scenarios. For each, presence vs. absence of seagrass was predicted by fitting a generalized linear model assuming a binomially distributed response and using a logit link function. Spatial autocorrelation identified using global Moran's I was accounted for using the residuals autocovariate (RAC) method[25]. Two scenarios are presented: 1) the full RAC model including the autocovariate term used for model prediction; and 2) parameters estimated using model (1), but predictions made with the autocovariate term set to zero.

A cross-validation procedure[14,23] was used to assess model performance by splitting the data set randomly into 75% for model fitting and 25% for model validation, repeated for 100 iterations for various threshold probability values, above which seagrass was classified as present. The threshold cut-off value was selected as the value where Kappa and Percent Correctly Classified were maximized [Supplemental 3].

Modification of bathymetry by SLR and accretion. SLR was modelled based on non-linearly increasing rates of SLR in decadal increments starting with 3 mm yr^{-1} in 2010. For each model run, the rate of increase of SLR varied between 0.5-3 mm $decade^{-1}$, to reach SLR of 45-135 cm by 2100. In each time-step, depth increased according to SLR, and the reef platform accreted vertically at a temporally uniform maximum rate of between 0 and 10 mm yr^{-1} [(20)], depending on scenario. If a location reached -1.2 m relative to mean sea level, equivalent to the shallowest presently observed depth of coral, it was prevented from accreting in that time-step. For illustrative purposes data are presented against four SLR trajectories representative of emissions scenarios[16,17] [Supplemental 4].

Prediction of seagrass distribution under future conditions. To predict habitat suitability for seagrass under future conditions, wave parameters for the modified bathymetries were re-calculated using SWAN, and the coefficients of the SDM used to predict seagrass presence in the future [Supplemental 5].

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Contributions

MIS, JXL, PJM, SRP, OHG, CEL designed the study.

MIS, CMR, JXL, CJB, SH, DPC, TB, CDW conducted the field work.

MIS, JXL, CMR, and SH provided input data.

MIS, DPC, AG, TB and CJB developed and ran the models.

MIS wrote the manuscript with input from all co-authors.

Competing financial interests

The authors declare no competing financial interests.

Figure Legends

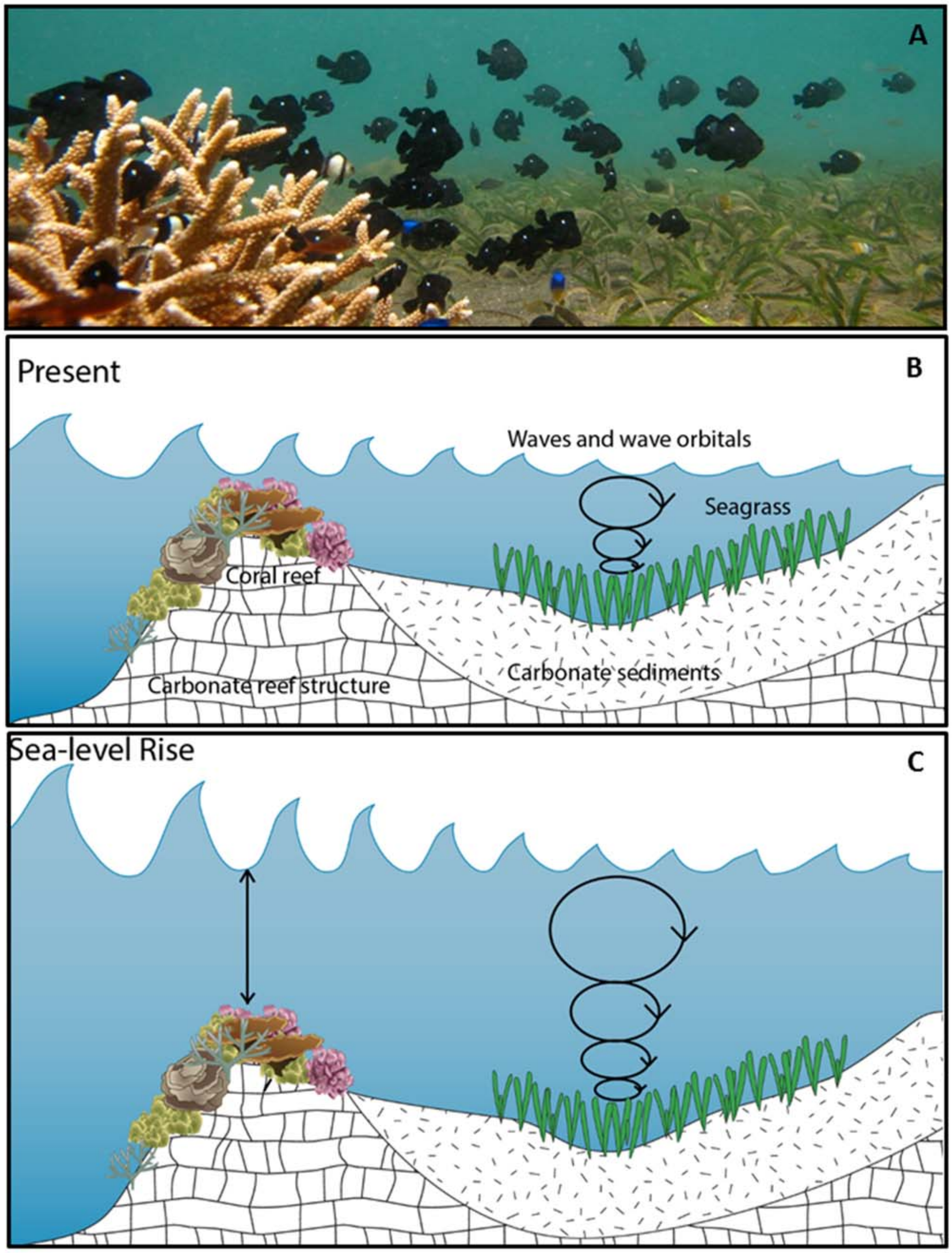

Figure 1. A) Seagrass and corals often live in close proximity in linked tropical marine ecosystems. B) Coral reefs block and dissipate wave energy and permit less wave tolerant

seagrass to exist in protected lagoons. C) Deepening water from sea-level rise (SLR) will allow larger more energetic waves to traverse the reef into the lagoon, which reduces habitat suitability for seagrass. Image credits: A) M.I. Saunders, B) IAN image gallery.

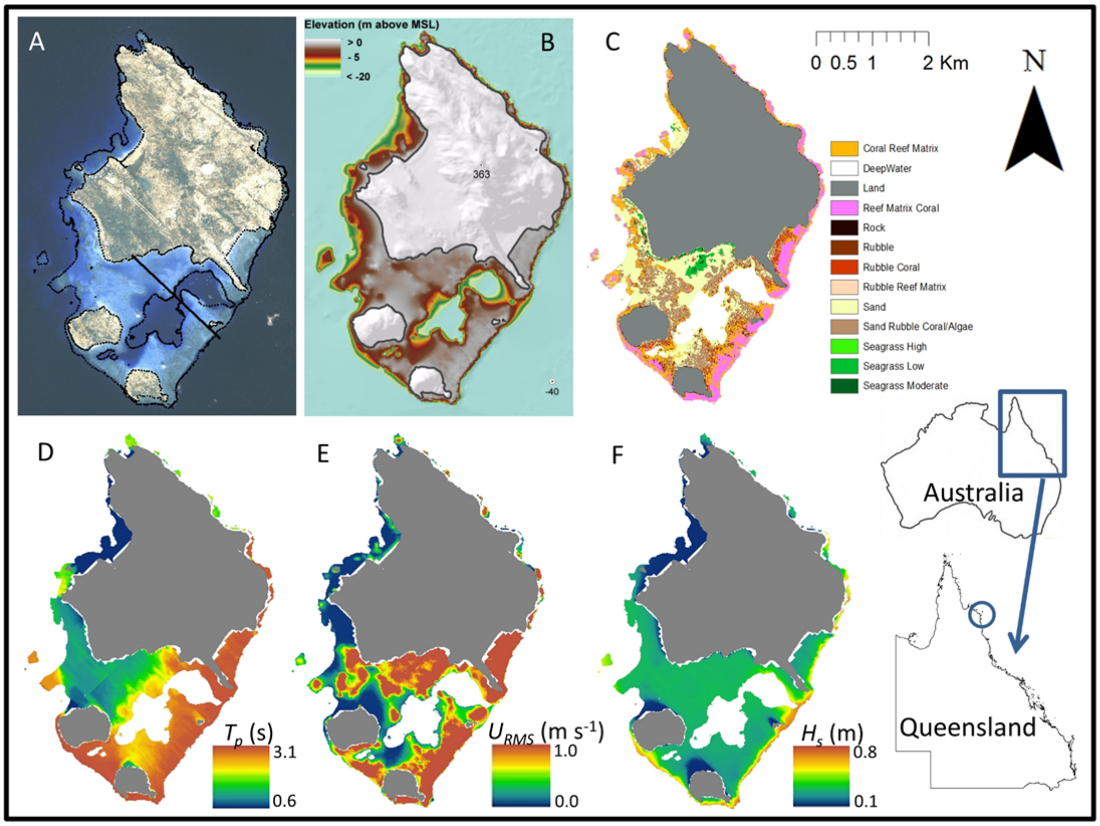

Figure 2. Study site and input data used to examine interdependent response of tropical marine habitats to sea-level rise, at Lizard Island, Great Barrier Reef, Australia. A) High resolution Worldview 2 satellite image of the study site obtained in October 2011, overlaid with a polygon indicating the boundaries of the shallow water (0-5 m) which were modelled in the 2D analyses (dashed black), and the transect line used in the 1D analyses (solid black). B) Digital Elevation Model (DEM)[21]; C) Benthic habitat maps produced using remote sensing techniques and field validation. D-F) Upper 90th percentiles of wave parameters. D = Peak wave period, s (T_p); E = Benthic wave orbital velocity, m s^{-1} (U_{RMS}); F = Significant wave height, m (H_s).

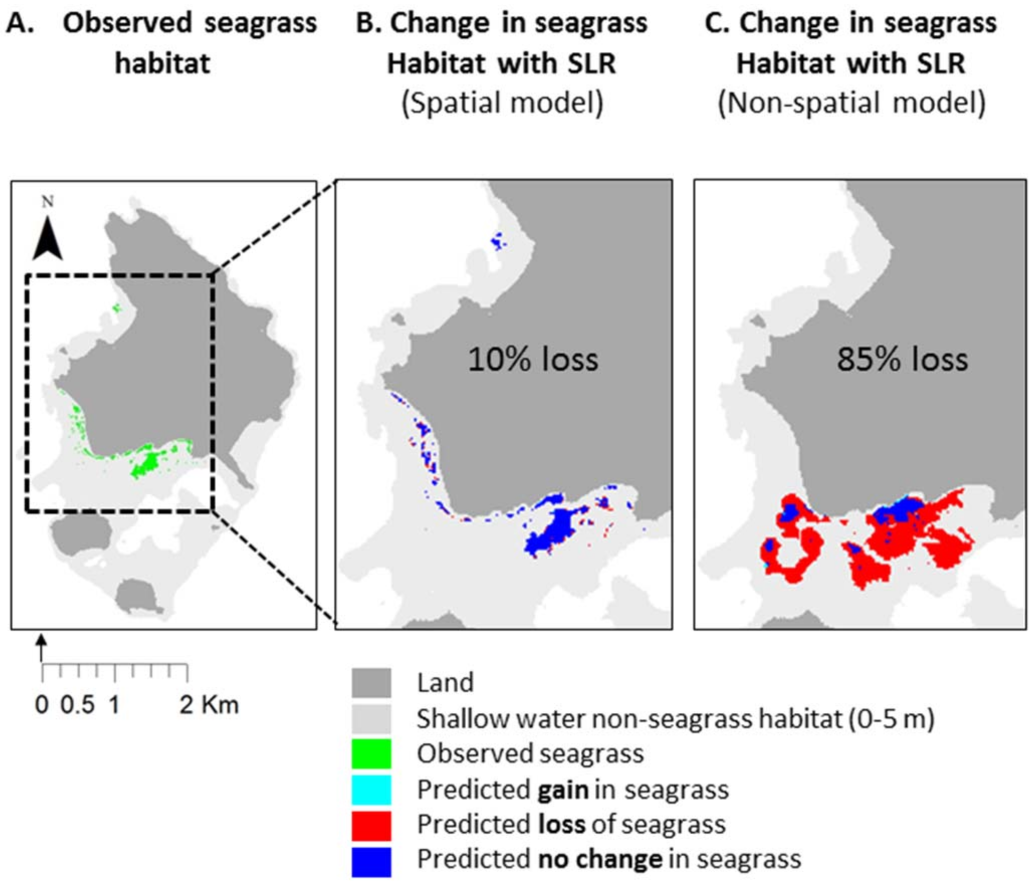

Figure 3. Results of modelling study examining the response of interdependent habitats (coral reefs and seagrass) to sea-level rise at Lizard Island, Great Barrier Reef. A) Observed seagrass presence mapped using remote sensing and field validation in 2011/2012; B) and C) show change in predicted seagrass suitable habitat based on wave parameters resulting from 1 m sea-level rise and no accretion of the benthos in reef or seagrass. B) "Spatial Model" – where present day spatial dependencies are maintained; C) "non-spatial model" – where spatial dependencies are omitted, reflecting potential for altered spatial relationships in future as conditions change. Predicted area of seagrass suitable habitat declines in both scenarios; with 10-85% less seagrass habitat compared to present day depending on assumptions about spatial dependencies.

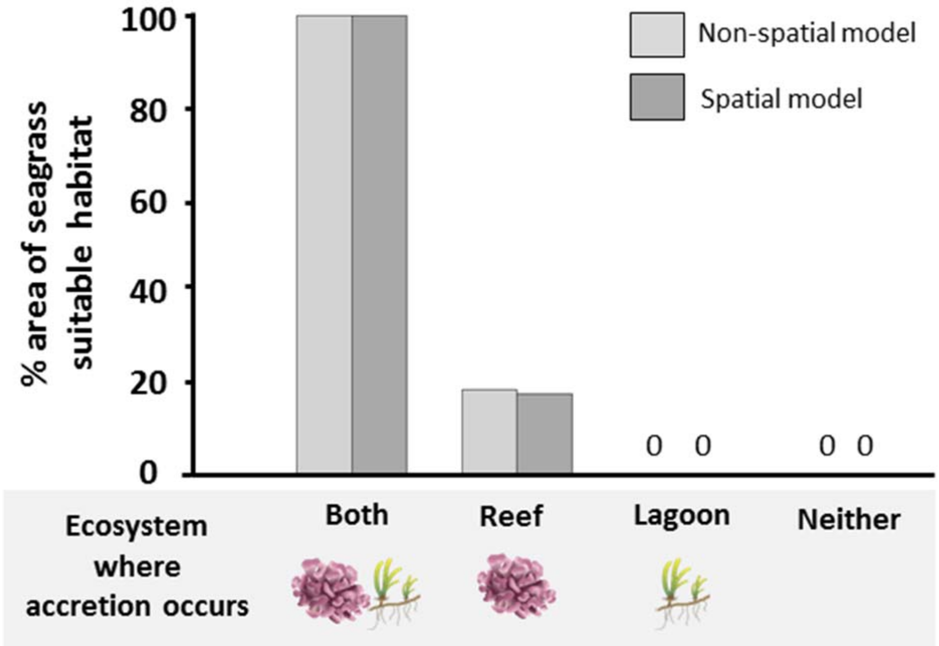

Figure 4. The relative (%) area of seagrass suitable habitat available along a transect across coral reef and seagrass habitats at Lizard Island, Great Barrier Reef. Results are for 4 scenarios of 1 m sea-level rise by 2100 and various combinations of ecosystem specific accretion of 1 m magnitude. Habitats become unsuitable for seagrass from 1m sea-level rise in scenarios where accretion does not occur on the coral reef.

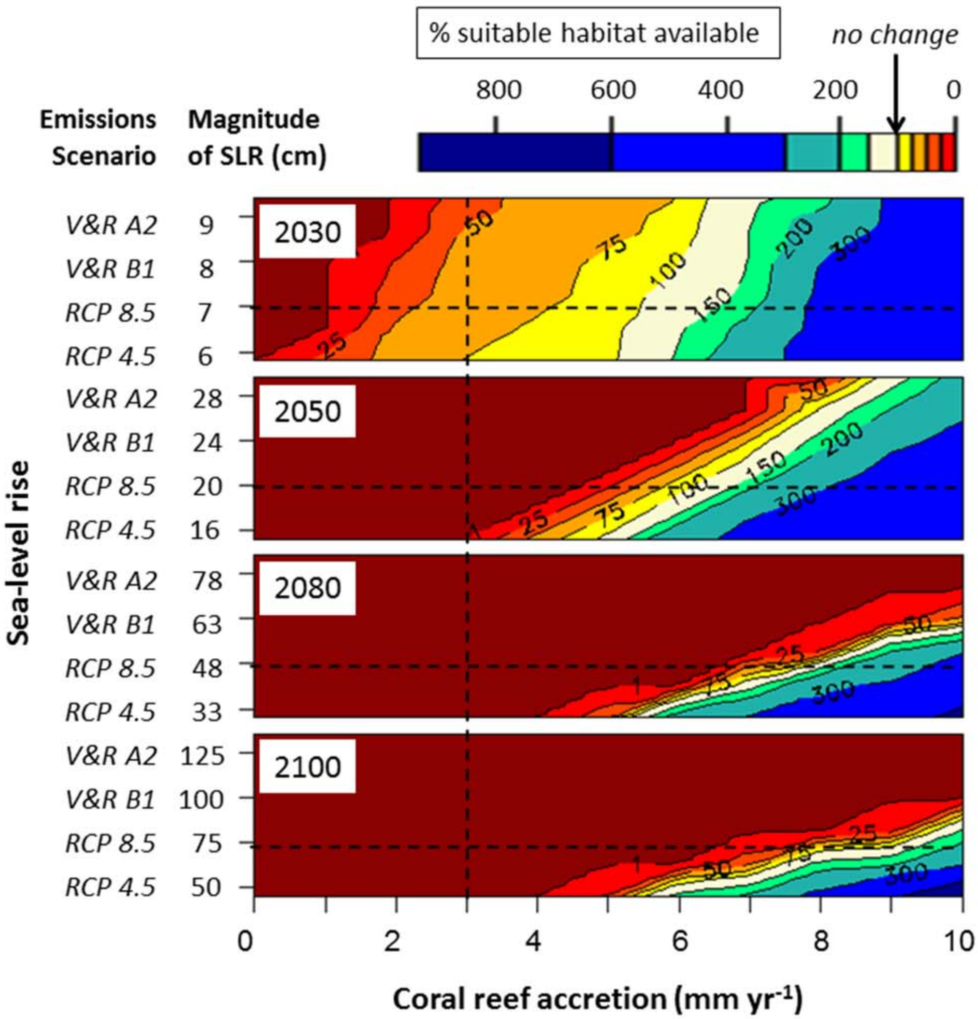

Figure 5. Relative (%) area of seagrass suitable habitat in 2030, 2050, 2080, and 2100, compared to present day, for a range of sea-level rise and coral reef accretion scenarios, with no accretion in seagrass. Sea-level rise is indicated by the magnitude (cm) occurring by that time step and by four corresponding emissions scenarios obtained from 2 sources (IPCC AR5[16]: RCP 4.5, RCP 8.5; Vermeer and Rahmstorf 2009[17]: V&R A1, V&R A2). Warm colours indicate losses and cool colours indicate gains, respectively, in area of suitable seagrass habitat relative to present day. Horizontal and vertical dashed lines indicates most likely SLR scenario given business as usual CO_2 emissions and maximum likely rate of coral reef platform accretion for healthy coral reefs[20].

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