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The potential of coastal ecosystems to mitigate the impact of sea-level rise in shallow tropical bays

L.M. Keyzer[a,*], P.M.J. Herman[a,b], B.P. Smits[b], J.D. Pietrzak[a], R.K. James[c], A.S. Candy[a,d], R.E. M. Riva[e], T.J. Bouma[c], C.G. van der Boog[a], C.A. Katsman[a], D.C. Slobbe[e], M. Zijlema[a], R. M. van Westen[f], H.A. Dijkstra[f]

[a] Environmental Fluid Mechanics, Civil Engineering and Geosciences, Delft University of Technology, Stevinweg 1, 2628 CN, Delft, the Netherlands
[b] Deltares, Marine & Coastal Systems, P.O. Box 177, 2600 MH, Delft, the Netherlands
[c] NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems and Utrecht University, P.O. Box 140, 4400 AC, Yerseke, the Netherlands
[d] NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, and Utrecht University, P.O. Box 59, 1790 AB, Den Burg, the Netherlands
[e] Geoscience and Remote Sensing, Delft University of Technology, Stevinweg 1, 2628 CN, Delft, the Netherlands
[f] Institute for Marine and Atmospheric Research, Utrecht University, Princetonplein 5, 3584 CC, Utrecht, the Netherlands

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ABSTRACT

Shallow tropical bays in the Caribbean, like Orient Bay and Galion Bay in Saint Martin, are often sheltered by coral reefs. In the relatively calm environment behind the reefs, seagrass meadows grow. Together, these ecosystems provide valuable ecosystem services like coastal protection, biodiversity hotspots, nursery grounds for animals and enhancing tourism and fisheries. However, sea-level rise imperils these ecosystems and the services they provide because of changing hydrodynamic conditions, with potential effects on the interdependencies between these ecosystems. By means of a hydrodynamic model that accounts for the interaction with vegetation (Delft3D Flexible Mesh), the impact of sea-level rise (0.87 m in 2100) is investigated for three scenarios of future reef development (i.e. keep-up, give-up and catch-up). If coral reefs cannot keep up with sea-level rise, the wave height and flow velocity increase significantly within associated bays, with the wave height doubling locally in case of eroding reefs in our model simulations. Since the presence of seagrass strongly depends on the hydrodynamic conditions, the response of seagrass to the future hydrodynamic conditions is projected using a habitat suitability model that is based on a logistic regression. The spatial character of the bays determines the response of seagrass. In Orient Bay, which is deeper and partly exposed to higher waves, the seagrass will likely migrate from the deeper parts to shallow areas that become suitable for seagrass because of the surf zone moving landward. In contrast, the conditions for seagrass worsen in Galion Bay for the catch-up and give-up scenario; due to the shallowness of this bay, the seagrass cannot escape to more suitable areas, resulting in significant seagrass loss. It is shown that healthy coastal ecosystems are able to limit the change in hydrodynamic conditions due to sea-level rise. Therefore, preserving these ecosystems is key for ensuring the resilience of shallow tropical bays to sea-level rise and maintaining their ecosystem services.

1. Introduction

In shallow tropical bays in the Caribbean, coral reefs and seagrass meadows are typically present. These ecosystems are linked through biological, chemical and physical processes (Gillis et al., 2014; Saunders et al., 2014). Waves break over the coral reefs, which enables seagrass to grow in the relatively calm, sheltered environment behind the reefs. Seagrass in turn provides nursery grounds for reef fish (Nagelkerken et al., 2002), functions as a pH buffer (James et al., 2019a; Unsworth et al., 2012) and filters nutrients and sediments (Gacia et al., 2002; Moore, 2004). Together, the ecosystems provide valuable ecosystem services. In addition to their ecological value, they form a natural flood protection. The coral reefs act as breakwaters, reducing the wave energy reaching the shoreline (Elliff and Silva, 2017). Seagrass meadows are able to attenuate flow and waves (Fonseca and Cahalan, 1992; Ondiviela et al., 2014), and to trap and stabilize sediment (Christianen et al., 2013;

* Corresponding author.
E-mail address: L.M.Keyzer@tudelft.nl (L.M. Keyzer).

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Duarte, 2002; Orth et al., 2006). James et al. (2019b) showed the potential role of seagrass in maintaining tropical beaches, which are important for the \$32.0 billion tourist industry in the Caribbean (World Tourism Organization, 2019).

However, global climate change threatens coastal ecosystems such as coral reefs and seagrass meadows (Hoegh-Guldberg and Bruno, 2010). The rate of seagrass loss is increasing worldwide (Waycott et al., 2009). Increased water depths due to sea-level rise may over time limit light availability and intensify wave action, which are both unfavourable for seagrass (de Boer, 2007). Seagrass's response to sea-level rise involves (i) adapting to new conditions, (ii) migrating to newly available areas, (iii) keeping its position relative to the water level through sediment accretion, or (iv) gradually eroding away if conditions become unsuitable (Duarte, 2002). As seagrass plays a key role in the functioning of coastal ecosystems (Duarte, 2002), its loss might affect the entire coastal system, including the beach as well as the coral reefs. Increased amounts of nutrients, sediments and pathogens following seagrass loss, and decreased food provision and nursery grounds for animals inhabiting both the seagrass and the reefs, may adversely impact the reefs (Gillis et al., 2014; Lamb et al., 2017).

The corresponding positive influence that coral reefs have on seagrass meadows, by providing a sheltered environment, is also endangered by global climate change. Coral reefs are under direct pressure due to rising water temperatures and ocean acidification (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Siegle and Costa, 2017). They may not be able to keep up with sea-level rise (Perry et al., 2018) which limits the depth-induced wave breaking on the reefs, and reef degradation reduces their frictional dissipating capacity (Principe et al., 2012). As a result, the hydrodynamic forces in the bay may increase, on top of the increase in water depth which results on itself in a relatively large increase in wave height. Thus, reef degradation will further enhance the hydrodynamic exposure of seagrass beds. As the collapse of one of the ecosystems thus negatively impacts the other ecosystem, a domino effect might be initiated, risking the loss of both ecosystems which will strongly enhance the risk of coastal erosion and loss of all other ecosystem services.

The interdependence between the neighbouring tropical marine ecosystems and hydrodynamic conditions is widely recognized. Saunders et al. (2014) indicated that the impact of sea-level rise cannot be assessed by modelling single ecosystems or the hydrodynamics only, since the seagrass distribution depends on the wave conditions that are in turn related to the surrounding reef height. In this study, we will use such a biogeomorphic modelling approach to assess the potential role of tropical marine ecosystems in mitigating the impact of sea-level rise on shallow tropical bays. To achieve this objective, we selected two contrasting bays in Saint Martin: a bay which is completely sheltered by surrounding reefs (Galion Bay) and a partly exposed bay (Orient Bay). A hydrodynamic model is set up with Delft3D Flexible Mesh (Kernkamp et al., 2011) forced by winds, tides and waves and including a vegetation module. To quantify the change in hydrodynamic conditions due to sea-level rise, simulations are done for three scenarios of future reef development (keep up, catch up and give up), covering the full range from healthy coral reefs that can keep up with sea-level rise (van Woesik et al., 2015) until degrading and eroding reefs (Hoegh-Guldberg et al., 2007; Hughes, 1994). Subsequently, the response of seagrass to the changed hydrodynamic conditions is determined using a habitat suitability model that is based on a logistic regression. This approach will give insight in the interdependence of hydrodynamic conditions and ecosystems and will improve the understanding of the response of shallow tropical bays to sea-level rise. The results can be used to derive protection strategies for the ecosystems in order to preserve their services.

2. Methods

2.1. Site description and climatology

Orient Bay and Galion Bay (Fig. 1a) are located on the eastern coast of Saint Martin, which is one of the Leeward Islands located in the northeast of the Caribbean (18.06° N, 63.05° W). Both bays are shallow with water depths not exceeding 10 and 5 m respectively (Fig. 1b). Whereas Galion Bay is completely surrounded by reefs, the northern part of Orient Bay is not, exposing this area to higher waves. These exposed areas are mainly bare, while the relatively calm areas behind the reefs are covered with seagrass meadows consisting of *Thalassia testudinum* and *Syringodium filiforme*. The calcifying algae *Halimeda* spp. are also found within the meadows. The bays experience a mixed, mainly diurnal tide with a range varying between 20 and 30 cm. Furthermore, the bays are exposed to the prevailing easterly winds that have an average speed of 5 m/s and swell waves coming from the Atlantic Ocean, which have an average height of 1.5 m.

2.2. Model description – Delft3D FM

A depth-averaged hydrodynamic model, called Delft3D Flexible Mesh (Delft3D FM), was used to simulate flow and waves driven by oceanic and meteorological forcing. An extensive description of the model can be found in Kernkamp et al. (2011). The model solves the depth-averaged shallow water equations on an unstructured grid. The wave module (D-Waves) is based on SWAN (Booij et al., 1999) and solves the discrete spectral action balance equation on a structured grid. By communicating with the flow module (D-Flow), water levels and flow velocities are updated and wave forces and Stokes drift are taken into account in the flow computations.

The effect of vegetation on the hydrodynamics is captured by the vegetation module in Delft3D FM. Flow attenuation is modelled using a modified bed roughness based on the work of Baptist (2005). To include wave dampening by vegetation, an additional energy dissipation term is implemented in SWAN by Suzuki et al. (2012) following the formulation of Mendez and Losada (2004). In this method, the energy loss due to vegetation is calculated as the work done by the drag forces of rigid cylinders on the fluid, neglecting the swaying of the vegetation.

2.3. Model setup – Delft3D FM

The flow was computed on a triangular grid with a resolution varying from 50 m at the coastal boundary to 150 m at the offshore boundary. The depth of each grid cell was derived by interpolating bathymetry data from three sources; local measurements were used in Galion Bay (James, 2018), the Navionics sonar chart provided the depths in Orient Bay and coarser GEBCO bathymetry data (Weatherall et al., 2015) was used offshore of the reefs. The reefs were included in the bathymetry and a locally increased bottom roughness was used in the flow model to represent the relatively high reef roughness. A Manning value of 0.07 $s/m^{1/3}$ was chosen such that the bottom friction coefficient becomes 0.02–0.05, which is similar to values found at other reefs (Lowe et al., 2009; Quataert et al., 2015). For bare sediment, the default Manning value of 0.023 $s/m^{1/3}$ was kept, while bed roughness at the seagrass meadows is determined by the vegetation module. The flexible time step is restricted by a maximum Courant number of 0.7. The closed western boundary formed the coastline, a water level condition representing the tide was imposed on the eastern boundary and the two lateral boundaries had Neumann boundary conditions such that water could move through freely. Tide, wind and waves forced the model. Although density-driven currents might occur due to, e.g., storm-related freshwater discharges, this forcing was excluded as this effect is assumed to be small. The tidal constituents were obtained using UTide (Codiga, 2011) and sea-level data (from: http://www.ioc-sealevelmonitoring.org/station.php?code=stmt). Using the three main tidal constituents

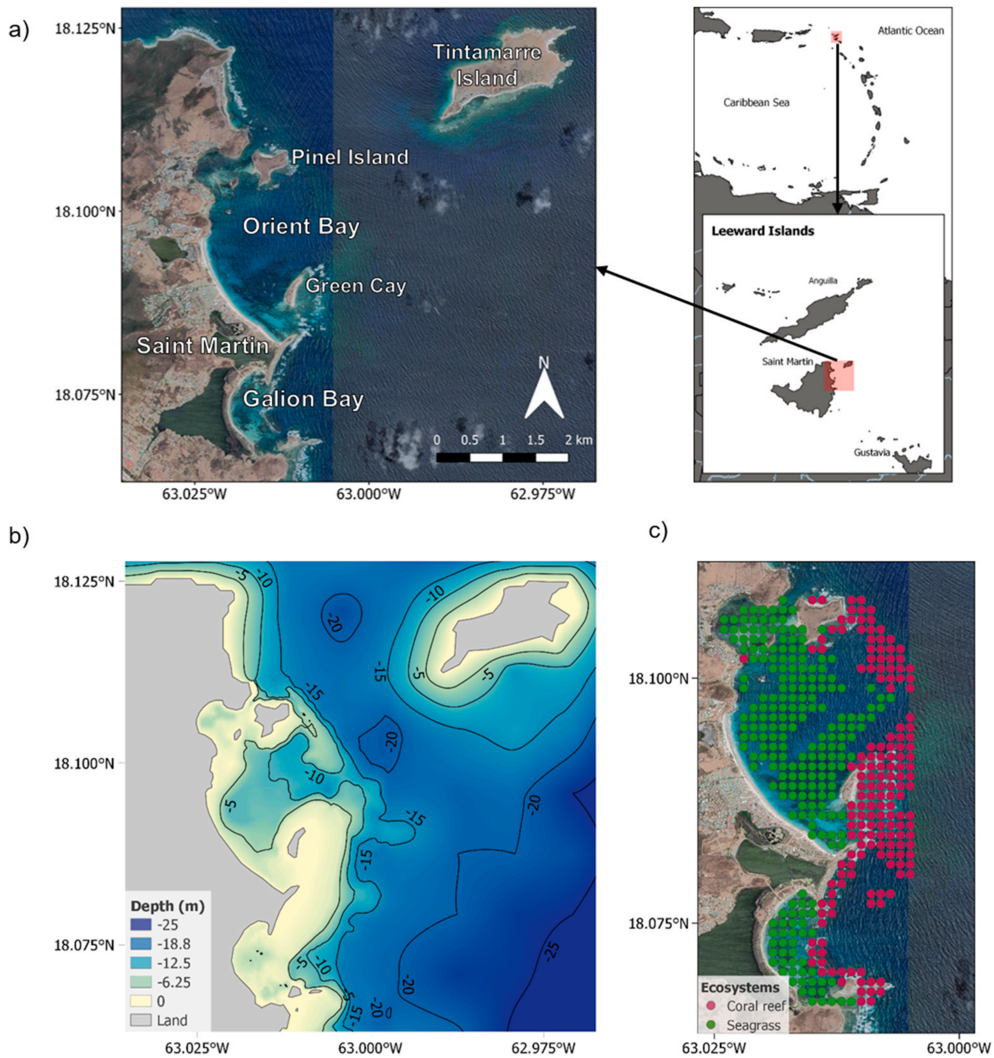

Fig. 1. Site overview of Orient Bay and Galion Bay, Saint Martin. (a) Aerial overview including toponyms. (b) Bathymetry: composed of measurements in Galion Bay (James, 2018), Navionics sonar chart in Orient Bay, and GEBCO data (Weatherall et al., 2015) offshore. (c) Presence of coral reefs and seagrass in Orient Bay and Galion Bay.

representing 91% of the tidal energy, K1, O1 and M2, the tidal signal was reconstructed.

Subsequently, the flow grid was nested in a larger wave grid with a resolution of 110 m, such that boundary effects of the wave model did not enter the flow model. Along the three boundaries of the wave model, a constant and uniform condition was prescribed, corresponding to average wave conditions (significant wave height (H_s) of 1.5 m, peak period (T_p) of 9 s and coming from the east). The high reef roughness could not be captured in the wave model. Furthermore, both the flow and wave model were forced using a uniform wind field that corresponds to average conditions (5 m/s, coming from the east). Every 2 h, the wave calculations were updated.

The seagrass was added in both the flow and wave model using the vegetation module, in which the vegetation height (89 mm if the water depth was less than 1.5 m, else 295 mm), the leaf width (8 mm if the water depth was less than 1.5 m, else 11 mm) and the density (constant value of 800 shoots/m^2) were defined based on measurements from James (2016). The flow drag coefficient was set to 1.0 based on the work of Nepf and Vivoni (2000) and a value of 0.1 was used for the wave drag coefficient, according to the formulation of Bradley and Houser (2009).

Using the model, the current hydrodynamic conditions were determined and subsequently how they change due to sea-level rise. However, the change in hydrodynamic conditions also depends on the response of the ecosystems, which in turn is determined by the altered physical forcing itself and by changing biological feedback mechanisms between seagrass and coral reefs. The sensitivity of the changing hydrodynamic conditions in the bays due to sea-level rise to the future reef development was assessed using three scenarios with varying reef height and roughness. The scenarios were based on the work of Neumann and Macintyre (1985) who classified the growth of coral reefs in three categories: (i) **keep up** if the reef growth rate equals the rate of sea-level rise, (ii) **catch up** in case the reef initially grows slower than the sea level rises but later reaches the stabilized or slower rising sea level, and (iii) **give up** whenever the reefs cannot follow the rising sea level and accretion stops and the reefs erode.

In this study, the keep-up scenario had a reef height that remained constant relative to sea level. This corresponds to an observed growth rate of healthy coral reefs (~10 mm/year) (Perry et al., 2018; van Woesik et al., 2015). In the catch-up scenario the absolute reef height was kept constant and thus equal to the present one (accretion equal to erosion), while for the give-up scenario the absolute reef height was decreased such that its depth relative to sea level increased by twice the amount of sea-level rise. The sea-level rise was assumed to be 0.87 m with respect to present day, which corresponds to the expected sea-level rise in the Caribbean for the year 2100 (Jevrejeva et al., 2016). Coastline retreat was not included.

2.4. Habitat suitability model

The presence of seagrass (Fig. 1c) depends strongly on the hydrodynamic conditions. Seagrass is absent in the deeper parts (>10 m) due to the limited light availability, and in the shallow parts along the coast because of wave action. The absence of seagrass also correlates to higher waves, in particular in the northeast corner of Orient Bay. To explore the effect of changing hydrodynamic conditions, we developed a habitat suitability model using R 3.5 (R Core Team, 2019). Seagrass occurrence was related to the current hydrodynamic conditions using a logistic regression. This relatively simple, yet flexible parametric modelling strategy was preferred over AI-based methods because of the limited size of the data set. A generalized linear model for a binomially distributed response variable (presence/absence), using a logit link, was applied to the observed seagrass presence/absence in each of the wave model grid cells. Independent variables used in the regression analysis were water depth, flow velocity, wave height, and the first-order interaction terms. Final model selection was based on minimizing the Akaike Information Criterion (AIC). The habitat suitability model predicts the probability of occurrence of seagrass, given the independent variables. The model, fitted on the actual conditions, was subsequently used to predict the probability of seagrass occurrence in the future, where future hydrodynamic conditions were derived from the hydrodynamic model runs.

3. Hydrodynamic model results

3.1. Current hydrodynamic conditions

In both the fully sheltered bay and the partly exposed bay, the circulation is mainly driven by the waves, and the wave height is controlled

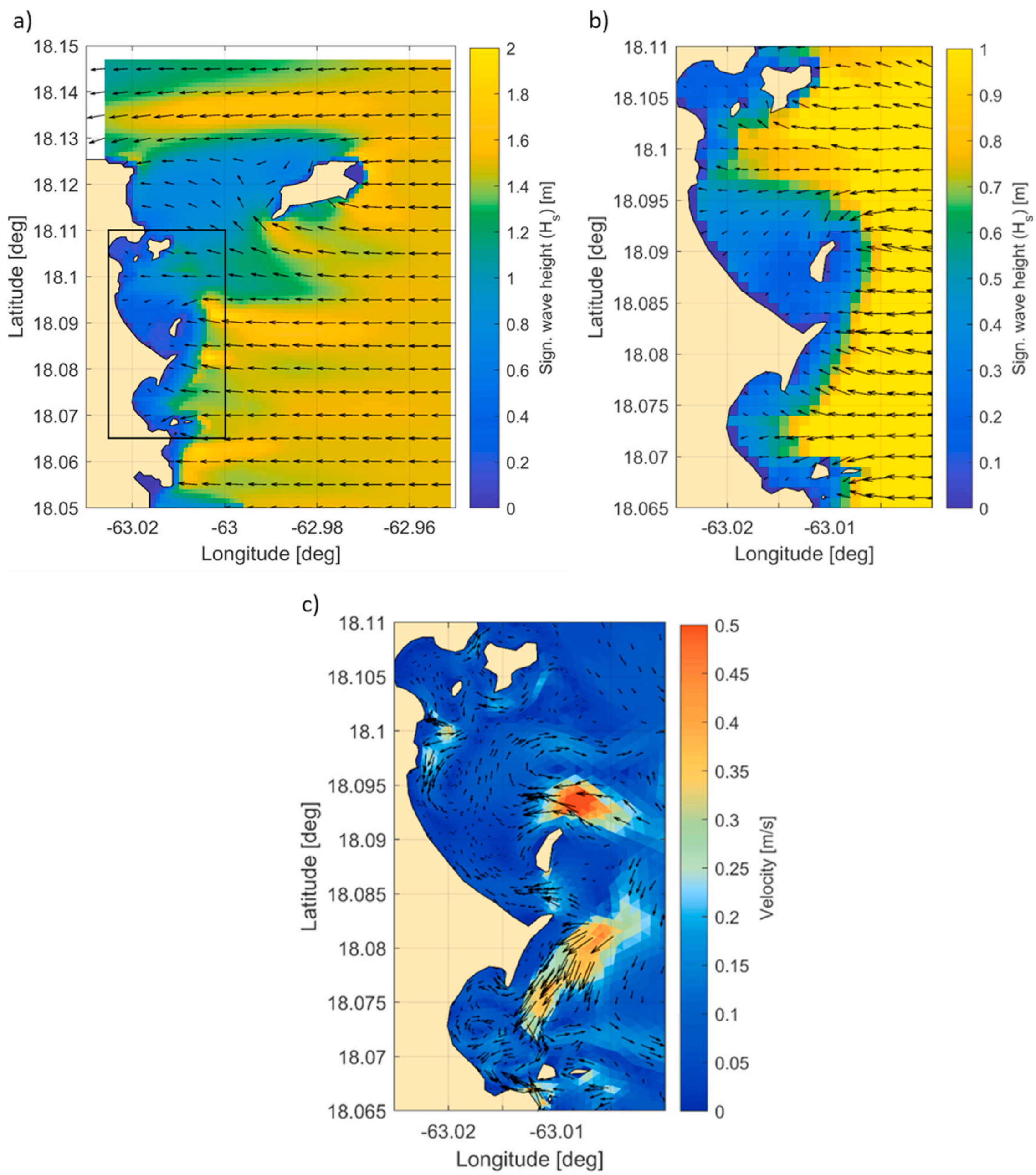

Fig. 2. Modelled hydrodynamic conditions in the current situation (time-averaged). (a) Significant wave height [m] under mean forcing ($H_s = 1.5$ m and $T_p = 9$ s). Arrows indicate wave direction. (b) Enlargement of bays, indicated by black box in (a). Note the different colourmap limits. (c) Depth-averaged flow velocity [m/s] and current vectors induced by the tide, the waves as shown in (a) and an easterly wind of 5 m/s.

by the reefs (Fig. 2). The reefs determine where the waves break and resulting currents flow into the bays. The bathymetry of the reefs also directs a return current back to the ocean. Lastly, the reef height in combination with the water level limits the wave height inside the bays, creating a sheltered environment. Looking at the wave height in Fig. 2a, the sheltering effect of Tintamarre Island is clearly visible with a reduced wave height between Pinel Island and Tintamarre Island (see Fig. 1 for locations). The effect of the reefs becomes clear after zooming in on the bays (Fig. 2b); shoaling is observed towards the reefs, the waves break on the reefs and a relatively calm wave environment is found behind the reefs. Under an easterly wind of 5 m/s and a wave height of 1.5 m at the boundary, the significant wave height is at most 0.5 m in Galion Bay, which is completely sheltered by reefs. The southern part of Orient Bay is protected by Green Cay and its surrounding reef, limiting the wave height to 0.5 m. The northern reef in front of Orient Bay lies deeper and is therefore less efficient in dissipating waves. Consequently, a significant wave height of 1.2 m is found in this area.

The currents in the bays, which are forced by the waves and an easterly wind of 5 m/s, strongly vary spatially (Fig. 2c). Strong currents up to 0.5 m/s are found above the reefs induced by wave breaking. The currents return to the ocean through the deeper gullies between the reefs with maximum velocities of 0.2 m/s. Although tide-induced currents in the bays are negligible (<0.01 m/s), the vertical motion of the tide influences the flow velocities, since the water depth above the reefs determines the wave height in the bays.

In Fig. 3, the influence of the seagrass on the hydrodynamic conditions is shown. Waves are dampened throughout both bays by the seagrass, and the effect is largest in the shallowest areas. At the shoreline, the wave height is reduced by 5–10%. The currents are mainly shifted, but not significantly attenuated. This is especially clear in Orient Bay, close to the coast and around the deeper gully. The effect of seagrass on the magnitude of the currents is relatively small (<5%).

3.2. *Impact of sea-level rise under different scenarios of future reef development*

Since a wave-driven circulation was found and the coral reefs protect the bays from incoming waves, the future reef development is expected to be the prime factor determining the impact of sea-level rise. A larger water depth reduces the wave dissipating ability of the reefs, leading to higher waves and stronger currents in the bays. In Fig. 4, this is shown for the three scenarios of future reef development (keep up, catch up and give up) after increasing the sea level by 0.87 m, under the same model assumptions. In case of the keep-up scenario, there is no change in wave height, and thus the flow velocities also remain approximately constant. Only in the exposed area just south of Pinel Island, there is a small increase in wave height. However, the significant wave height increases for the catch-up and give-up scenarios. Especially the wave height above the reefs increases, where the relative change in water depth is largest. The average wave height increased by 0.09 m and 0.15 m inside Galion Bay and by 0.08 m and 0.11 m inside Orient Bay for the catch-up and give-up scenario, respectively. Consequently, the flow velocities also increase. For the give-up scenario, they almost double in both bays.

To further illustrate the role of the coral reefs, the change in hydrodynamic conditions due to sea-level rise is compared at three different locations near the coast: a sheltered location in both bays and an exposed location in Orient Bay (Fig. 5a). Fig. 5b shows the relative impact of sea-level rise above the reefs at each location for the three different scenarios. If the coral reefs keep up with sea-level rise, the hydrodynamic conditions do not change significantly compared to the present-day conditions (Fig. 5c and d: keep-up scenario). Due to the increased water depth inside the bays, the wave height increases slightly, while the depth-averaged flow velocity decreases. But for the catch-up and keep-up scenario, there is a change in water depth above the reefs, which is relatively largest for the shallowest reefs (Fig. 5b). Therefore, larger waves enter the bays (Fig. 5c) and flow velocities increase (Fig. 5d). At the sheltered location in Galion Bay, the wave height increased by 40% for the catch-up scenario and 60% for the give-up scenario. At the sheltered location in Orient Bay, the wave height increased by more than a factor of 2 for the catch-up scenario and by more than a factor of 3 for the give-up scenario. This highlights that the impact of sea-level rise strongly depends on the future reef development, and not only on the amount of sea-level rise itself.

Furthermore, the relative impact is different for the three locations. The change in hydrodynamic conditions is relatively small for the exposed location, which is located behind an opening in the reef(indicated by circle in Fig. 5). However, the wave height and flow velocity increase significantly at the sheltered locations (indicated by triangle and square in Fig. 5), underscoring the importance of the protecting function of coral reefs.

4. Seagrass distribution

In the different scenarios, the seagrass distribution was assumed to be unaffected. However, it is widely known that the presence of seagrass depends strongly on the hydrodynamic conditions (de Boer, 2007). Therefore, we assessed the impact of the changing hydrodynamic

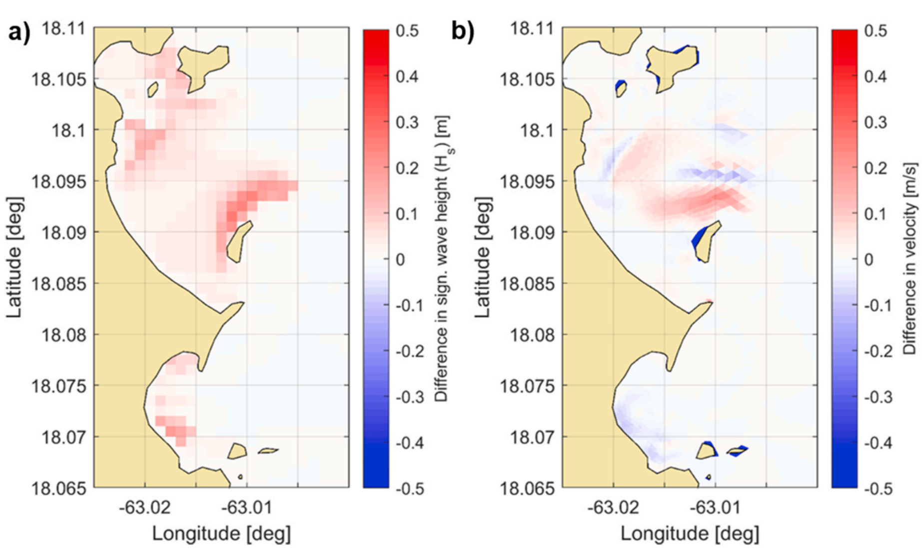

Fig. 3. Effect of seagrass on hydrodynamic conditions. (a) Difference in wave height (m). (b) Difference in flow velocity (m/s).

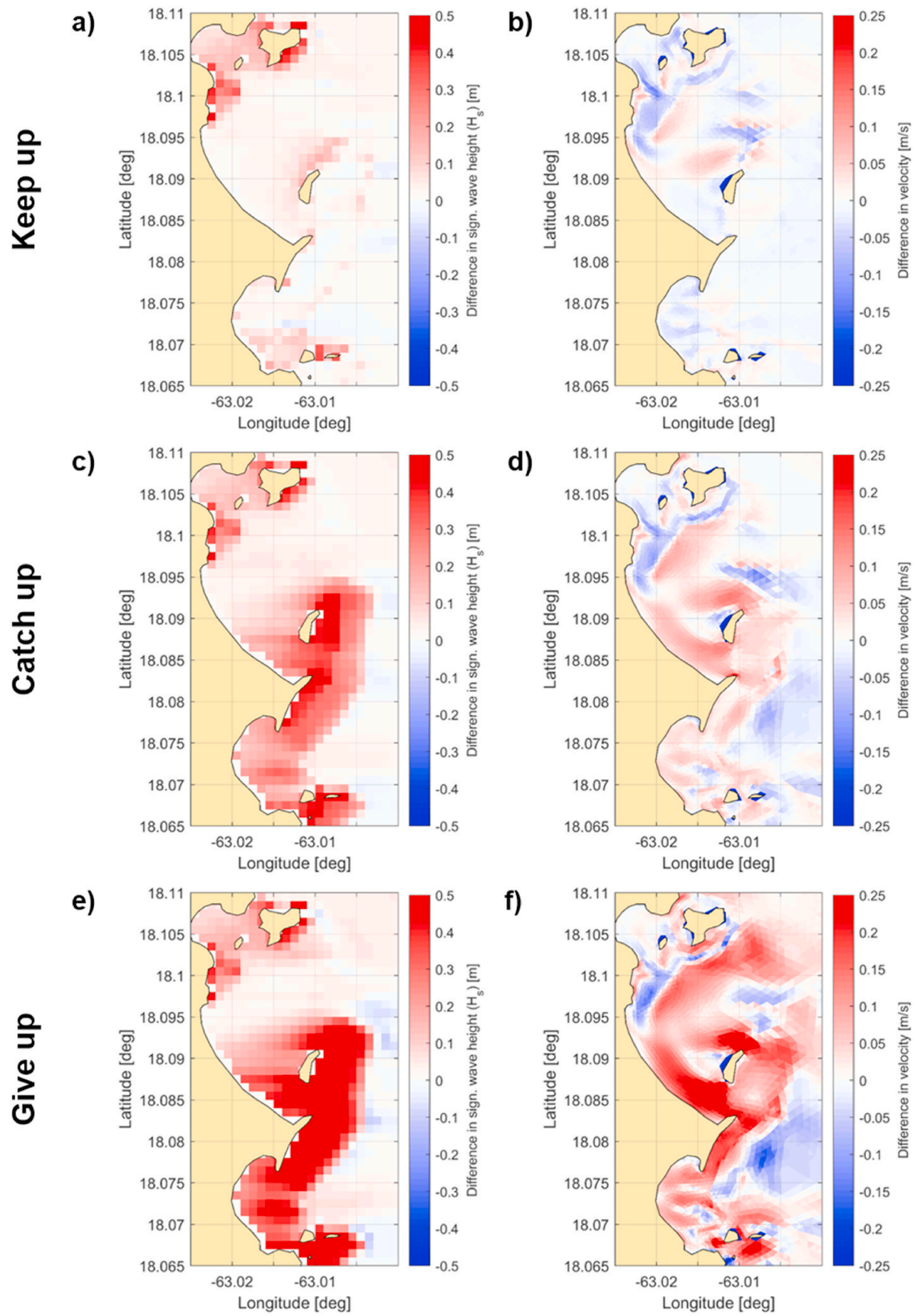

Fig. 4. Change in (a, c, e) significant wave height [m] and (b, d, f) flow velocity [m/s] due to sea-level rise (0.87 m) for each scenario (keep up, catch up and give up), compared to the present-day conditions.

conditions on the presence of seagrass for the different scenarios by means of a habitat suitability model.

4.1. Model evaluation

First, the model was fitted against the observed presence of seagrass (Fig. 6a) and current hydrodynamic conditions (Fig. 2). Starting from the full model, the least significant terms were consecutively dropped, until the lowest AIC was reached (see supplementary Table S1). The included variables in the final model were water depth (linear and squared), flow velocity (linear and squared) and wave height (linear only), and the first-order interaction between flow velocity and wave height. The wave height squared and the other interaction terms were excluded due to non-significance. The resulting response curves can be found in supplementary Figure S1.

As can be seen in Fig. 6 and Table 1, the modelled seagrass distribution shows a high level of agreement with the actual one; the overall accuracy of the model is 77.9% and a kappa value of 0.44 is achieved. The model, however, tends to overestimate the presence of seagrass near the coast and in the deep gully in Orient Bay. The latter could be a

Table 1
Overall model accuracy, model precision (kappa statistic), true presence and true absence at the study site predicted by our habitat suitability model.

Area	Accuracy	Kappa statistic	True presence	True absence
Total	77.9%	0.44	92.3%	47.6%
Orient Bay	75.9%	0.43	91.0%	49.0%
Galion Bay	89.6%	0.24	97.7%	20.0%

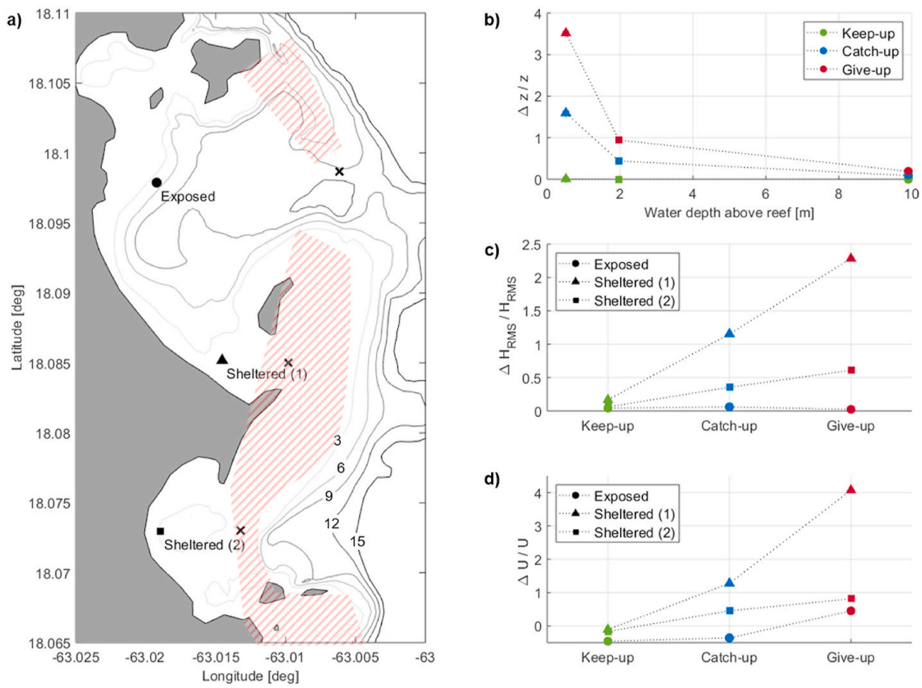

Fig. 5. Impact of sea-level rise for the different scenarios of coral reef growth at three locations. (a) The locations: an exposed and sheltered location in Orient Bay and a sheltered location in Galion Bay, indicated by a circle, triangle and square, respectively. The bathymetry contours (3 m interval, only depths up to 15 m shown) are plotted and the locations of the reefs are highlighted (red stripes). The crosses indicate the locations where the water depth above the reef is taken. For the exposed location, the water depth is taken in the opening between the reefs. The relative change in (b) water depth above the reef, (c) wave height and (d) flow velocity compared to the present-day situation at each location is shown for the three scenarios: keep-up (green), catch-up (blue), give-up (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

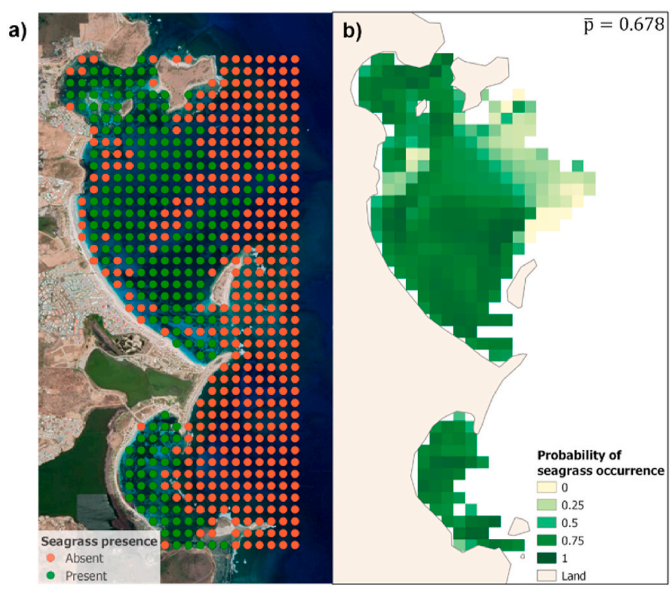

Fig. 6. (a) Spatial map of seagrass presence. (b) Probability of seagrass occurrence for current situation as predicted by the logistic regression model, which has been fitted to the seagrass distribution (a) and the hydrodynamic conditions (Fig. 2).

consequence of using a depth-averaged hydrodynamic model instead of a 3D model such that near-bed currents were underestimated. But the absence of seagrass could also be caused by natural disturbances, e.g. grazing turtles, or human activities, such as fishing or boat anchoring, rather than due to the hydrodynamic conditions. The relatively low true absence in Galion Bay (and thus the poorer Kappa value) is caused by the very few grid cells where seagrass is absent (5/48).

4.2. Projection to future scenarios

When the coral reefs kept up with sea-level rise, the change in hydrodynamic conditions was limited (Fig. 4a and b). This explains why the results of the habitat suitability model do not show significant changes in the occurrence of seagrass for the keep-up scenario (Fig. 7a and b; Table 2). Due to the increased water depth, the wave action reduces close to the shore, improving the conditions for seagrass near the coast in both bays. In the deeper parts of Orient Bay, the strength of light limitation increases slightly, reducing the probability of seagrass occurrence and leading to a small loss of seagrass (−1.9%). Since the water depth above the reefs remained constant, the wave conditions did not change. Therefore, no seagrass is lost just behind the reefs in both bays. In Galion Bay, the amount of seagrass even slightly increases by 4.3%, because of newly suitable area near the coast.

For the catch-up scenario (Fig. 7c and d; Table 2), seagrass is predicted to shift in Orient Bay from the deeper parts to the newly suitable areas near the coast. The probability of seagrass occurrence decreases in the deeper parts, where light availability becomes the limiting factor, while the probability increases in the shallow parts close to the shore. Here, the conditions become more favourable because of the landward moved surf zone due to the increased water depth. In Galion Bay, there is a small decrease in the probability of seagrass occurrence (−0.075), which leads to a seagrass loss of 15.2%. This indicates the potential vulnerability of the seagrass and the entire coastal system of a shallow tropical bay.

In the give-up scenario (Fig. 7e and f; Table 2), even more seagrass is lost (−23.9%). In Orient Bay, the impact is largest just behind the reefs due to the increased wave height. Furthermore, a shift in seagrass occurrence from the deeper to the shallower parts is predicted, similar to what was found for the catch-up scenario. Overall, a seagrass loss of 20.7% is predicted for Orient Bay, while 39.1% of the seagrass is predicted to be lost in Galion Bay. In Galion Bay, the seagrass cannot escape to newly suitable areas due to a strong increase in hydrodynamic forces across the entirety of the bay.

In the scenario simulations, the seagrass was assumed to remain present, and thus continued to attenuate the flow and waves in the bays, while we found that especially for the give-up scenario a significant amount of seagrass will be lost. Fig. 8 presents the results of the give-up scenario without seagrass. Compared to the give-up scenario with seagrass (Fig. 7e and f), the probability of seagrass occurrence decreases even more and leads to an additional 15.7% loss of seagrass. This also shows that it is harder to recover for seagrass once it is gone, which is

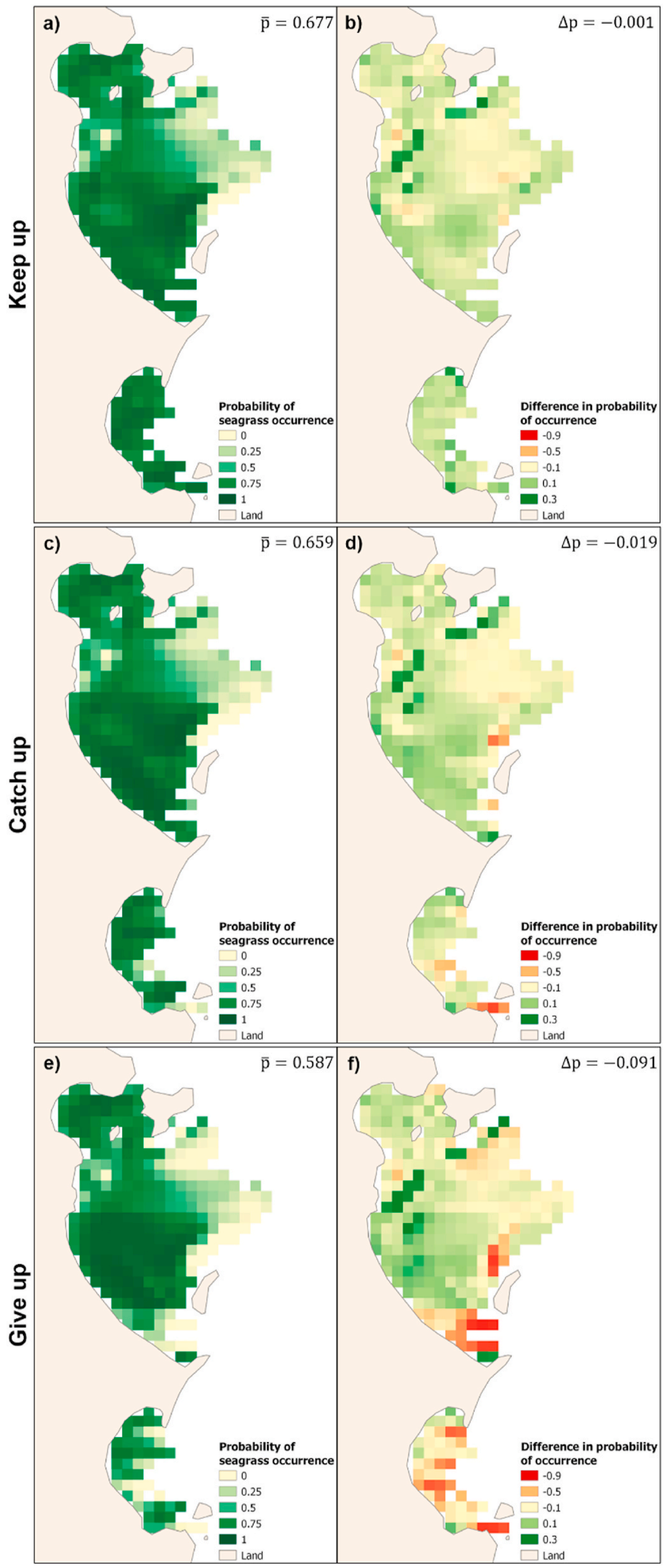

Fig. 7. Predicted probability of seagrass occurrence for (a) the keep-up, (c) catch-up and (e) give-up scenario. (b,d,f) Change in probability of occurrence for each scenario compared to the current situation (Fig. 5b).

most likely in the sheltered parts (Galion Bay and southern part of Orient Bay). However, even in this worst-case scenario, 70.7% of the seagrass will survive.

Table 2
Predicted changes in seagrass area in the study area for the keep-up, catch-up and give-up scenario.

Area	Keep-up scenario	Catch-up scenario	Give-up scenario
All	+0.8%	−4.6%	−23.9%
Orient Bay	0.0%	−2.3%	−20.7%
Galion Bay	+4.3%	−15.2%	−39.1%

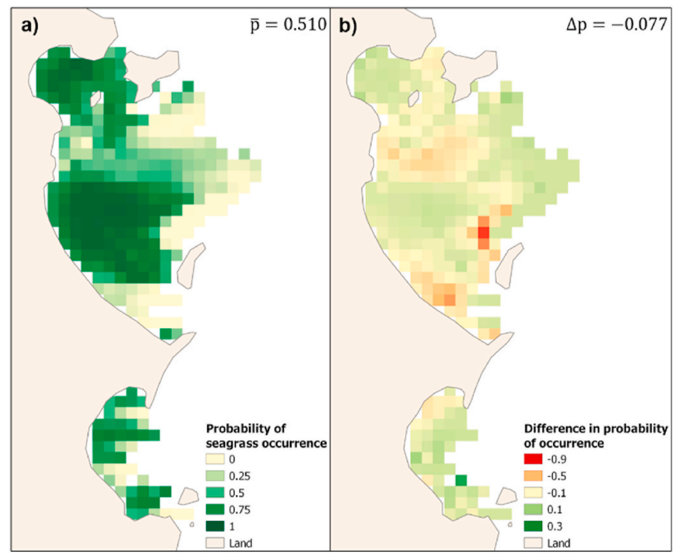

Fig. 8. (a) Predicted probability of seagrass occurrence for the give-up scenario, assuming there is no seagrass. (b) Change in probability of occurrence compared to the give-up scenario, including seagrass (Fig. 6e).

5. Discussion

It can be expected that sea-level rise will significantly affect the hydrodynamic and ecological conditions in shallow tropical bays, where the relative impact of sea-level rise compared to the present-day water depth is very large. Our model explorations assuming 0.87 m sea-level rise and including three scenarios for future reef development (i.e. keep up, catch up and give up), confirm that the hydrodynamic conditions change significantly if the coral reefs cannot keep up with sea-level rise. The wave height doubles locally in the case of eroding reefs. Moreover, it shows that tropical marine ecosystems are able to modulate the system's response to sea-level rise. Healthy coral reefs can limit the change in hydrodynamic conditions, i.e. the mean wave height inside the bays increased less than 0.05 m in the keep-up scenario. This enables seagrass to keep growing in the sheltered bays, which further attenuates flow and waves.

5.1. Interdependence of ecosystems

The interdependence of coral reefs and seagrass meadows and their impact on the hydrodynamic conditions are a key factor in the resilience of tropical shallow bays with respect to sea-level rise. Firstly, coral reefs limit the change in hydrodynamic conditions directly by dissipating wave energy (Moberg and Folke, 1999). Our study shows that if the coral reefs keep up with the rising sea level such that the water depth above the reefs will not increase, the hydrodynamic conditions will not change significantly; currents within the studied bays are almost exclusively wave-driven, and the wave height is primarily determined by the wave dissipation over the reefs. However, global trends show that more and more coral reefs are affected by the consequences of climate change, making it unlikely that they are indeed able to keep up with sea-level rise (Perry et al., 2018). Our catch-up and give-up scenario explore the impact of vertical growth deficiency in the coral reefs. These scenarios show significant changes in the hydrodynamic conditions as soon as water depth over the reefs increased due to the wave-driven circulation. This impact is large for bays where the circulation is wave-driven, but could be smaller for tide- or wind-dominated bays.

As demonstrated by our habitat suitability model, the presence of seagrass depends strongly on the hydrodynamic conditions. It can be anticipated that changes in hydrodynamic conditions will directly affect the seagrass distribution. The habitat suitability model predicts a strong dependence of the (future) seagrass distribution on the future reef development. The loss of seagrass, in turn, could have profound consequences for the coral reefs, because biological and chemical feedback mechanisms could be disturbed (Gillis et al., 2014; Unsworth et al., 2012). Possible consequences are decreased buffering of pH, increased suspended sediment concentrations, lowered water quality and the disappearance of nursery grounds for reef fish, which can further worsen the conditions for the reefs. However, although our models predict loss of seagrass in the scenarios where reefs cannot keep up with sea-level rise, the losses are not complete and are partly compensated by newly suitable seagrass habitat, particularly in Orient Bay. Therefore, no complete loss of the seagrass-coral reef interaction is expected that might lead to domino effects on the entire coastal system.

Comparisons of the different scenarios shows that the future vertical accretion rate of the coral reefs is the key factor determining hydrodynamics and ecology of the shallow coastal bay systems. Our results indicate that, in case of healthy coral reefs, the loss of seagrass due to the altered hydrodynamic conditions under 0.87 m sea level rise is negligible. Thus, coral reefs can be regarded as a first line of defence against sea-level rise.

5.2. Response of coral reefs

In the case of healthy coral reefs, the accretion rates match the rate of sea-level rise (Perry et al., 2018; van Woesik et al., 2015). However, coral reefs are declining globally, and especially in the Caribbean, due to global climate change, i.e. rising water temperatures and ocean acidification, and direct human stresses, i.e. overfishing and pollution (Wilkinson, 2008). Coral bleaching, triggered by increased water temperatures (Hoegh-Guldberg, 1999), will occur more frequently and become more severe (Heron et al., 2016; Hoegh-Guldberg et al., 2007), limiting the reef growth. Therefore, there is a high risk that coral reefs risks will not keep up with sea-level rise (Perry et al., 2018).

In shallow reefs, the temperature at the corals' surface can be up to 1 °C higher than the ambient water temperature during low tide and weak flow conditions due to the presence of a thermal boundary layer (Fabricius, 2006; Jimenez et al., 2008). If the coral reefs cannot keep up with sea-level rise, the flow velocities and water depth above the reefs will increase, as our model results show. Stronger flow conditions will reduce the thickness of the thermal boundary layer and thus reduce the likelihood of exceeding the critical water temperature (Jimenez et al., 2011). The increased water depth will, in addition, limit the irradiance reaching the corals' surface, reducing the heating. Therefore, we hypothesize that sea-level rise on itself could contribute to the resilience of coral reefs to warming oceans, although they are already suffering from the consequences of global climate change. However, our model did not resolve or parametrize the thermal boundary layer, and neither did it include coral reef growth. More research on this topic would be needed to test this inference.

5.3. Response of seagrass

In addition to its ecological value, seagrass also contributes to coastal protection (Duarte, 2002; James et al., 2019b), which is becoming increasingly important because of sea-level rise (Luijendijk et al., 2018). Under conditions of moderate to severe degradation of the coral reefs, the response of the seagrass to the altered hydrodynamic conditions depends on the spatial characteristics of the bays. Our habitat suitability model shows that seagrass is likely to shift from deeper to shallower parts in Orient Bay, where the spatial heterogeneity allows the seagrass to migrate and adapt to the new conditions, ensuring the resilience of the seagrass. Contrastingly, more seagrass is lost in Galion Bay. The combination of the complete sheltering by reefs and the relatively uniform shallowness ensures tolerable conditions nowadays. However, we have seen that for the catch-up and give-up scenario the wave height increased, exceeding the tolerable wave height for seagrass, leaving little escape for the seagrass. Thus, the spatial character of a bay could provoke a different response of seagrass to changing conditions.

By attenuating waves and reducing suspended sediment concentrations, seagrass improves the surrounding conditions (Duarte, 2002). This implies that once the seagrass is gone, the conditions worsen further making the growth and recolonisation of seagrass even harder (Olesen, 1996; van der Heide et al., 2011, 2007). Our habitat suitability model showed that the probability of seagrass occurrence indeed decreased based on the hydrodynamic conditions after removing the seagrass.

5.4. Morphological response

Although the morphology of the bays is currently stable, evaluating the morphodynamics is potentially important. Depending on future reef development, we have seen that the seagrass distribution could change significantly. This could result in erosion, as there is less seagrass to trap and stabilize sediment. With a greater area of exposed seafloor, erosion, either due to hurricanes on the short term or changing wave conditions on the long term, could cause further loss of seagrass through burial or uprooting (Cabaço et al., 2008). Furthermore, changes in suspended sediment concentrations due to increased wave height and stronger currents could affect the seagrass meadows by reducing the light availability (e.g. Olesen, 1996) and smother the coral reefs (e.g. Hoegh-Guldberg, 1999). But sedimentation could also be beneficial for seagrass, since reduced water depths improve the light availability. Coral reefs and calcifying algae are both a source of sediment (James et al., 2019b), which could stimulate the accretion. Because our model could not take morphodynamic changes into account, further research on the sediment dynamics of shallow tropical bays is therefore recommended to predict the response of the ecosystems more accurately.

5.5. Implications for management of shallow tropical bays

Sea-level rise poses a risk to shallow tropical bays, endangering their valuable ecosystem services. Our model results show that coastal protection is prominent among these services. The present and future state of the bays is entirely dependent on the feedback from the reefs and seagrass on waves and currents. This has important consequences for local economic activity. Tourism and fisheries can negatively impact seagrass and coral reefs through physical disturbance. In the longer term, however, local industries crucially depend on the conservation of these ecosystems. As climate-driven factors are hard to manage locally (Scheffer et al., 2001), focus should be on reducing the human impact on shallow tropical bays such that they maintain their natural resilience. Installing sewage treatment plants, prohibiting the removal of seagrass, allowing seagrass to migrate and protecting the coral reefs against tourists, ships, and fishing activities are examples of possible measures. In case the coral reefs die and erode, they could be replaced by artificial reef structures, which have already successfully been applied in different areas (Harris, 2009; Silva et al., 2016). Hydrodynamic and habitat suitability models could be utilised to identify vulnerable areas and the locations where artificial reef structures would provide the most benefit. In this study, the south of Orient Bay and the entire border of Galion Bay would be particularly vital regions to retain a reef.

6. Conclusion

Healthy ecosystems can ensure the resilience of shallow tropical bays such as Orient and Galion Bays to sea-level rise. Since a wave-driven circulation was found in the bays, the change in hydrodynamic conditions due to sea-level rise strongly depends on future reef development. As soon as the sea level rises faster than the reefs grow vertically, the wave height increases and subsequently the flow velocities too. The seagrass is expected to withstand or adapt to these changed hydrodynamic conditions. Depending on the spatial character of the bay, seagrass shifts from the deeper waters, where light availability is limited, to shallower areas, where wave action is reduced, or disappears after tolerable conditions are exceeded. But overall, it is predicted that seagrass will not be completely lost due to the changing hydrodynamic conditions.

In this paper, we have shown that the impact of sea-level rise on shallow tropical bays strongly depends on the persistence of tropical marine ecosystems, with the coral reefs as first line of defence and the seagrass meadows as their support. These ecosystems form a natural flood protection, which becomes increasingly important due to sea-level rise. In addition, long-term sustainability of economic activities, such as fisheries and tourism, crucially depends on the healthy preservation of these ecosystems. Therefore, the conservation of the ecosystems is critically important for countries with shallow tropical bays.

Author statement

LK and PH designed the study. LK and BS developed the hydrodynamic model and processed the data. PH developed the habitat suitability model. RJ collected field data. LK analysed the results and drafted the manuscript. PH, BS, JP, AC and RR supervised the work. All authors discussed the results and commented on the manuscript. This work is part of the research program ALW-Caribbean with project 858.14.061 (SCENES), which is financed by the Netherlands Organisation for Scientific Research (NWO).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.107050.

References

Baptist, M.J., 2005. Modelling Floodplain Biogeomorphology. PhD Thesis. Delft University of Technology.
Booij, N., Ris, C., Holthuijsen, L.H., 1999. A third-generation wave model for coastal regions 1. Model description and validation. J. Geophys. Res. Ocean. 104, 7649–7666.
Bradley, K., Houser, C., 2009. Relative velocity of seagrass blades: implications for wave attenuation in low-energy environments. J. Geophys. Res. 114 https://doi.org/10.1029/2007JF000951.
Cabaço, S., Santos, R., Duarte, C.M., 2008. The impact of sediment burial and erosion on seagrasses: a review. Estuar. Coast Shelf Sci. https://doi.org/10.1016/j.ecss.2008.04.021.
Christianen, M.J.A., van Belzen, J., Herman, P.M.J., van Katwijk, M.M., Lamers, L.P.M., van Leent, P.J.M., Bouma, T.J., 2013. Low-canopy seagrass beds still provide important coastal protection services. PloS One 8. https://doi.org/10.1371/journal.pone.0062413.
Codiga, D.L., 2011. Unified Tidal Analysis and Prediction Using the UTide Matlab Functions. Narragansett. https://doi.org/10.13140/RG.2.1.3761.2008. RI.
de Boer, W.F., 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. Hydrobiologia 591, 5–24. https://doi.org/10.1007/s10750-007-0780-9.
Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29, 192–206. https://doi.org/10.1017/S0376892902000127.
Elliff, C.I., Silva, I.R., 2017. Coral reefs as the first line of defense: shoreline protection in face of climate change. Mar. Environ. Res. 127, 148–154. https://doi.org/10.1016/j.marenvres.2017.03.007.
2006 Fabricius, K.E., 2006. Fabricius, Katharina E.. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: implications for coral bleaching?. Limnol. Oceanogr. 51 (1), 30–37. Limnol. Oceanogr. 51, 30–37.
Fonseca, M.S., Cahalan, J.A., 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast Shelf Sci. 35, 565–576. https://doi.org/10.1016/S0272-7714(05)80039-3.
Gacia, E., Duarte, C.M., Middelburg, J.J., 2002. Carbon and nutrient deposition in a Mediterranean seagrass (Posidonia oceanica) meadow. Limnol. Oceanogr. 47, 23–32. https://doi.org/10.4319/lo.2002.47.1.0023.
Gillis, L.G., Bouma, T.J., Jones, C.G., Van Katwijk, M.M., Nagelkerken, I., Jeuken, C.J.L., Herman, P.M.J., Ziegler, A.D., 2014. Potential for landscape-scale positive interactions among tropical marine ecosystems. Mar. Ecol. Prog. Ser. 503, 289–303. https://doi.org/10.3354/meps10716.
Harris, L.E., 2009. Artificial reefs for ecosystem restoration and coastal erosion protection with aquaculture and recreational amenities. Reef J 1, 235–246.
Heron, S.F., Maynard, J.A., Van Hooidonk, R., Eakin, C.M., 2016. Warming trends and bleaching stress of the world's coral reefs 1985-2012. Sci. Rep. 6 https://doi.org/10.1038/srep38402.
Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshw. Res. 50, 839–866. https://doi.org/10.1071/MF99078.
Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328, 1523–1528. https://doi.org/10.1126/science.1189930.
Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1743.
Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551. https://doi.org/10.1126/science.265.5178.1547.
James, R.K., 2016. Seagrass Measurements. Unpublished raw data.
James, R.K., 2018. Bathymetric Survey Galion Bay. Saint Martin. Unpublished raw data.
James, R.K., Katwijk, M.M., Tussenbroek, B.I., Heide, T., Dijkstra, H.A., Westen, R.M., Pietrzak, J.D., Candy, A.S., Klees, R., Riva, R.E.M., Slobbe, C.D., Katsman, C.A., Herman, P.M.J., Bouma, T.J., 2019a. Water motion and vegetation control the pH dynamics in seagrass-dominated bays. Limnol. Oceanogr. 1–14 https://doi.org/10.1002/lno.11303.
James, R.K., Silva, R., Van Tussenbroek, B.I., Escudero-Castillo, M., Mariño-Tapia, I., Dijkstra, H.A., Van Westen, R.M., Pietrzak, J.D., Candy, A.S., Katsman, C.A., Van Der Boog, C.G., Riva, R.E.M., Slobbe, C., Klees, R., Stapel, J., Van Der Heide, T., Van Katwijk, M.M., Herman, P.M.J., Bouma, T.J., 2019b. Maintaining tropical beaches with seagrass and algae: a promising alternative to engineering solutions. Bioscience 69, 136–142. https://doi.org/10.1093/biosci/biy154.
Jevrejeva, S., Jackson, L.P., Riva, R.E.M., Grinsted, A., Moore, J.C., 2016. Coastal sea level rise with warming above 2 °C. Proc. Natl. Acad. Sci. Unit. States Am. 113, 13342–13347. https://doi.org/10.1073/pnas.1605312113.
Jimenez, I.M., Kühl, M., Larkum, A.W.D., Ralph, P.J., 2011. Effects of flow and colony morphology on the thermal boundary layer of corals. J. R. Soc. Interface 8, 1785–1795. https://doi.org/10.1098/rsif.2011.0144.
Jimenez, I.M., Kühl, M., Larkum, A.W.D., Ralph, P.J., 2008. Heat budget and thermal microenvironment of shallow-water corals: do massive corals get warmer than branching corals? Limnol. Oceanogr. 53, 1548–1561. https://doi.org/10.4319/lo.2008.53.4.1548.
Kernkamp, H.W.J., Van Dam, A., Stelling, G.S., de Goede, E.D., 2011. Efficient scheme for the shallow water equations on unstructured grids with application to the Continental Shelf. Ocean Dynam. 61, 1175–1188. https://doi.org/10.1007/s10236-011-0423-6.
Lamb, J.B., Van De Water, J.A.J.M., Bourne, D.G., Altier, C., Hein, M.Y., Fiorenza, E.A., Abu, N., Jompa, J., Harvell, C.D., 2017. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. Science 355, 731–733. https://doi.org/10.1126/science.aal1956.
Lowe, R.J., Falter, J.L., Monismith, S.G., Atkinson, M.J., 2009. Wave-driven circulation of a coastal reef-lagoon system. J. Phys. Oceanogr. 339, 873–893. https://doi.org/10.1175/2008JPO3958.1.
Luijendijk, A., Hagenaars, G., Ranasinghe, R., Baart, F., Donchyts, G., Aarninkhof, S., 2018. The state of the world's beaches. Sci. Rep. 8 https://doi.org/10.1038/s41598-018-24630-6.
Mendez, F.J., Losada, I.J., 2004. An empirical model to estimate the propagation of random breaking and nonbreaking waves over vegetation fields. Coast. Eng. 51, 103–118. https://doi.org/10.1016/j.coastaleng.2003.11.003.
Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9.
Moore, K.A., 2004. Influence of seagrasses on water quality in shallow regions of the lower chesapeake bay. J. Coast Res. 45, 162–178. https://doi.org/10.2112/si45-162.1.
Nagelkerken, I., Roberts, C.M., Van der Velde, G., Dorenbosch, M., Van Riel, M.C., Cocheret de la Moriniere, E., Nienhuis, P.H., 2002. How important mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Mar. Ecol. Prog. Ser. 244, 299–305. https://doi.org/10.3354/meps244299.
Nepf, H.M., Vivoni, E.R., 2000. Flow structure in depth-limited, vegetated flow. J. Geophys. Res. 105, 28547–28557. https://doi.org/10.1029/2000JC900145.

Neumann, A.C., Macintyre, I., 1985. Reef response to sea level rise: keep-up, catch-up or give-up. In: Proceedings of the Fifth International Reef Congress, pp. 105–110.
Olesen, B., 1996. Regulation of light attenuation and eelgrass Zostera marina depth distribution in a Danish embayment. Mar. Ecol. Prog. Ser. 134, 187–194. https://doi.org/10.3354/meps134187.
Ondiviela, B., Losada, I.J., Lara, J.L., Maza, M., Galván, C., Bouma, T.J., van Belzen, J., 2014. The role of seagrasses in coastal protection in a changing climate. Coast. Eng. 87, 158–168. https://doi.org/10.1016/j.coastaleng.2013.11.005.
Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K. L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987. https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2.
Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S., Manzello, D.P., Morgan, K.M., Slangen, A.B.A., Thomson, D.P., Januchowski-Hartley, F., Smithers, S.G., Steneck, R.S., Carlton, R., Edinger, E.N., Enochs, I.C., Estrada-Saldívar, N., Haywood, M.D.E., Kolodziej, G., Murphy, G.N., Pérez-Cervantes, E., Suchley, A., Valentino, L., Boenish, R., Wilson, M., Macdonald, C., 2018. Loss of coral reef growth capacity to track future increases in sea level. Nature 558, 396–400. https://doi.org/10.1038/s41586-018-0194-z.
Principe, P.P., Bradley, P., Yee, S.H., Fisher, W.S., Johnson, E.D., Allen, P., Campbell, D. E., 2012. Quantifying Coral Reef Ecosystem Services. Washington, DC.
Quataert, E., Storlazzi, C., van Rooijen, A., Cheriton, O., van Dongeren, A., 2015. The influence of coral reefs and climate change on wave-driven flooding of tropical coastlines. Geophys. Res. Lett. 42, 6407–6415. https://doi.org/10.1002/2015GL064861.
Saunders, M.I., Leon, J.X., Callaghan, D.P., Roelfsema, C.M., Hamylton, S., Brown, C.J., Baldock, T., Golshani, A., Phinn, S.R., Lovelock, C.E., Hoegh-Guldberg, O., Woodroffe, C.D., Mumby, P.J., 2014. Interdependency of tropical marine ecosystems in response to climate change. Nat. Clim. Change 4, 724–729. https://doi.org/10.1038/nclimate2274.
Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature. https://doi.org/10.1038/35098000.
Siegle, E., Costa, M.B., 2017. Nearshore wave power increase on reef-shaped coasts due to sea-level rise. Earth's Futur. 5, 1054–1065. https://doi.org/10.1002/2017EF000624.
Silva, R., Mendoza, E., Mariño-Tapia, I., Martínez, M.L., Escalante, E., 2016. An artificial reef improves coastal protection and provides a base for coral recovery. J. Coast Res. 75, 467–471. https://doi.org/10.2112/SI75-094.1.
Suzuki, T., Zijlema, M., Burger, B., Meijer, M.C., Narayan, S., 2012. Wave dissipation by vegetation with layer schematization in SWAN. Coast. Eng. 59, 64–71. https://doi.org/10.1016/j.coastaleng.2011.07.006.
Unsworth, R.K.F., Collier, C.J., Henderson, G.M., McKenzie, L.J., 2012. Tropical seagrass meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean acidification. Environ. Res. Lett. 7, 9. https://doi.org/10.1088/1748-9326/7/2/024026.
van der Heide, T., Van Nes, E.H., Geerling, G.W., Smolders, A.J.P., Bouma, T.J., van Katwijk, M.M., 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10, 1311–1322. https://doi.org/10.1007/s10021-007-9099-7.
van der Heide, T., van Nes, E.H., van Katwijk, M.M., Olff, H., Smolders, A.J.P., 2011. Positive feedbacks in seagrass ecosystems – evidence from large-scale empirical data. PloS One 6, e16504. https://doi.org/10.1371/journal.pone.0016504.
van Woesik, R., Golbuu, Y., Roff, G., 2015. Keep up or drown: adjustment of western Pacific coral reefs to sea-level rise in the 21st century. R. Soc. Open Sci. 2, 150181. https://doi.org/10.1098/rsos.150181.
Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. U.S.A. 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106.
Weatherall, P., Marks, K.M., Jakobsson, M., Schmitt, T., Tani, S., Arndt, J.E., Rovere, M., Chayes, D., Ferrini, V., Wigley, R., 2015. A new digital bathymetric model of the world's oceans. Earth Sp. Sci. 2, 331–345. https://doi.org/10.1002/2015EA000107.
Wilkinson, C., 2008. Status of Coral Reefs of the World: 2008. Townsville, Australia.
World Tourism Organization, 2019. International Tourism Highlights, 2019 Edition. UNWTO, Madrid, Spain. https://doi.org/10.18111/9789284421152.