



Climate change mitigation by coral reefs and seagrass beds at risk: How global change compromises coastal ecosystem services



R.K. James ^{a,b,*}, L.M. Keyzer ^c, S.J. van de Velde ^{b,d}, P.M.J. Herman ^{c,e}, M.M. van Katwijk ^f, T.J. Bouma ^{a,g}

^a Department of Estuarine & Delta Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, Yerseke, the Netherlands

^b Bgeosys, Department of Geoscience, Environment and Society, Université Libre de Bruxelles, Brussels, Belgium

^c Environmental Fluid Mechanics, Civil Engineering and Geosciences, Delft University of Technology, Delft, the Netherlands

^d Operational Directorate Natural Environment, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

^e Marine & Coastal Systems, Deltares, Delft, the Netherlands

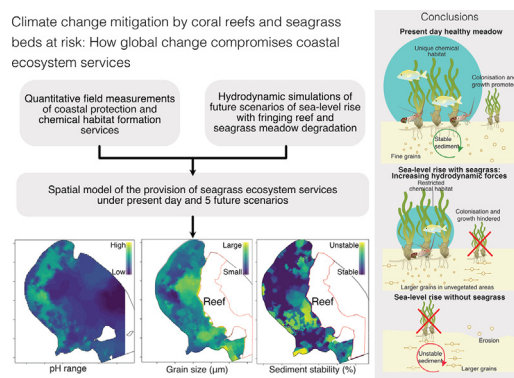
^f Department of Environmental Science, Institute for Water and Wetland Research, Faculty of Science, Radboud University Nijmegen, Nijmegen, the Netherlands

^g Faculty of Geosciences, Department of Physical Geography, Utrecht University, Utrecht, the Netherlands

HIGHLIGHTS

- Sea-level rise could lessen the provision of seagrass ecosystem services.
- Field study, spatial and physical modelling used to quantify changes in services.
- Loss of seagrass meadows would exacerbate climate change effects on tropical coasts.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Jacopo Bacenetti

Keywords:

pH refugia
Thalassia testudinum
 Sea-level rise
 Habitat degradation
 Coastal ecology
 Caribbean
 Tropical ecosystem

ABSTRACT

Seagrass meadows provide valuable ecosystem services of coastal protection and chemical habitat formation that could help mitigate the impact of sea level rise and ocean acidification. However, the intensification of hydrodynamic forces caused by sea level rise, in addition to habitat degradation threaten the provision of these ecosystem services. With quantitative field measurements of the coastal protection and chemical habitat formation services of seagrass meadows, we statistically model the relationships between hydrodynamic forces, vegetation density and the provision of these ecosystem services. Utilising a high-resolution hydrodynamic model that simulates end of the century hydrodynamic conditions and three scenarios of coral reef degradation (i.e., keep up, remain or loss) we quantify how the environmental conditions within a tropical bay will change given changes to the provision of ecosystem services. Our study shows that increasing hydrodynamic forces lead to a seafloor made up of a larger grain size that is increasingly unstable and more vulnerable to erosion. The loss of a fringing reef leads to larger hydrodynamic forces entering the bay, however, the 0.87 m increase in depth due to sea-level rise reduces the bed shear stress in shallower areas, which limits the change in the ecosystem services provided by the current benthic seagrass meadow. Loss of seagrass constitutes the greatest change in a bay ecosystem, resulting in the sediment surface where seagrass existed becoming unstable and the median sediment grain size increasing by 5–7%. The loss of seagrass also leads to the disappearance of the unique fluctuating chemical habitat, which leaves the surrounding community vulnerable to ocean acidification. A

* Corresponding author at: Faculté des Sciences, Campus du Solbosch - CP 160/02, Avenue F.D. Roosevelt, 50, 1050 Bruxelles, Belgium.
 E-mail address: Rebecca.james@ulb.be (R.K. James).

<http://dx.doi.org/10.1016/j.scitotenv.2022.159576>

Received 16 August 2022; Received in revised form 14 October 2022; Accepted 15 October 2022

Available online 21 October 2022

0048-9697/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

reduction or complete loss of these ecosystem services would impact the entire community assemblage while also leaving the surrounding coastline vulnerable to erosion, thus exacerbating negative effects brought about by climate change.

1. Introduction

Coastal regions are experiencing unprecedented and rapid change due to both climate change and local anthropogenic disturbances. Ecosystem services provided by natural coastal communities could help mitigate the increased risk imposed by climate change on coastal regions (Sutton-Grier et al., 2015; Morris et al., 2018; James et al., 2019b; Noisette et al., 2022). The effectiveness of these ecosystem services is, however, dependent upon the health and density of the natural community providing the service and the spatial extent that its presence impacts the surrounding environment (James et al., 2019a; Noisette et al., 2022). Given the ongoing degradation of coastal environments (Orth et al., 2006; Waycott et al., 2009; Burke et al., 2011; Jackson et al., 2014) along with rising sea levels which deepen and subsequently cause an increase in the hydrodynamic forces within current coastal habitats (Storlazzi et al., 2011; Keyzer et al., 2020), the ecosystem services provided by coastal communities are at risk. Quantifying how the provision of these increasingly important ecosystem services provided by coastal communities will respond to further habitat degradation and sea-level rise is vital for analysing the future risks facing coastal regions.

Through their physical presence and metabolism, natural coastal communities can provide ecosystem services that benefit surrounding organisms, including human communities (Anthony et al., 2011; Saunders et al., 2014; Hurd, 2015; James et al., 2019a). Two such community types are seagrass meadows and coral reefs. Their physical presence attenuates waves and stabilises sediment, providing an important coastal protection service for tropical coastal regions (Arkema et al., 2013; Saunders et al., 2014; Quataert et al., 2015; James et al., 2019b). At the same time, by altering the local seawater carbonate chemistry through their metabolism, both coral reefs and seagrass meadows create a unique chemical habitat with fluctuating carbonate chemistry conditions (Hendriks et al., 2014; James et al., 2019a; Noisette et al., 2022). These fluctuations in the pH do not significantly change the mean pH, but instead create temporary periods of high and low pH throughout a diurnal cycle (James et al., 2019a). Given the ongoing lowering of seawater pH, termed ocean acidification, the temporary high pH/high aragonite saturation state conditions created by this metabolism have been proposed as potential refugia for calcifying organisms and early larval stages of fish and molluscs (Frieder et al., 2014; Hurd, 2015; Kapsenberg et al., 2018; Wahl et al., 2018). The research regarding these metabolic-driven fluctuations acting as pH refugia still remains inconclusive due to also creating low pH conditions at night (Hurd et al., 2011; Cornwall et al., 2013; Britton et al., 2016; Mangan et al., 2017; Koweek et al., 2018; Falkenberg et al., 2021). However, these fluctuations in the carbonate chemistry might, in consequence, increase the resilience of populations to ocean acidification, with Pansch et al. (2014) showing that barnacle populations inhabiting areas with large fluctuations are more tolerant to elevated CO₂ conditions than populations from stable environments. Whatever the effect that these fluctuations in the seawater carbonate chemistry may have on the surrounding community, they are a natural dynamic of coastal vegetated ecosystems and therefore are considered part of the habitat-forming ecosystem service of these communities. The sheltered environment with a stable sediment surface and dynamic carbonate chemistry created by coral reefs and seagrass meadows supports a rich diversity of organisms (Nagelkerken and van der Velde, 2003; Saunders et al., 2014), including valuable fishery and keystone species (Unsworth et al., 2019).

The provision of ecosystem services by coral reefs and seagrass meadows is dependent upon local physical factors that affect the abundance and metabolic rates of the communities, while hydrodynamic forces impact the spatial extent that is influenced by the ecosystem service (James

et al., 2019a; Noisette et al., 2022). The wave and flow attenuation capabilities of hard structures, such as coral reefs, or flexible canopies like seagrass meadows are greatest when the organisms' density is high and there is a low ratio of water depth to reef or vegetation height (Ward et al., 1984; Paul et al., 2012; Shields et al., 2017; James et al., 2020b). Sediment stabilisation by rooted vegetation is another important factor contributing to coastal protection in coastal ecosystems, however, this is again dependent upon the vegetation density (Potouroglou et al., 2017; James et al., 2020a). While shoot density of seagrass meadows and the level of water refreshment surrounding the canopy directly impact the magnitude and spatial extent that the metabolism of seagrass meadows affects the surrounding environment, and thus, the extent of the unique chemical habitat (James et al., 2019a; Noisette et al., 2022). These interactions suggest that the current ecosystem services provided by coastal communities will be negatively impacted by both increasing hydrodynamic forces due to sea-level rise and by habitat degradation.

Tropical coral reefs and seagrasses are under threat (Hoegh-Guldberg et al., 2007; Quataert et al., 2015; Siegle and Costa, 2017). Local stressors such as eutrophication, over-fishing, sedimentation and physical damage from boating activities have reduced the resilience of much of the world's tropical coral reef and seagrass ecosystems (Orth et al., 2006; Hoegh-Guldberg et al., 2007; Hughes et al., 2017a). The pressures on these coastal ecosystems are being further exacerbated by rising sea surface temperature (Oliver, 2019; Oliver et al., 2021), heatwaves (Meehl and Tebaldi, 2004; Hughes et al., 2017b; Smale et al., 2019), intensifying storms, and ocean acidification (Anthony et al., 2008; Jokiel et al., 2008). These local and global stressors combined are causing widespread degradation in both coral reefs and seagrass ecosystems (Hughes, 1994; Orth et al., 2006; Waycott et al., 2009; Hughes et al., 2017a). Coral reefs have been proposed to respond to climate change in three ways: 'Keep-up', 'Remain', or 'Give-up' (Neumann and Macintyre, 1985; Elliff and Silva, 2017). The 'Keep-up' fringing reef scenario is where the vertical accretion rate of coral reefs is sufficient to keep up with sea level rise. This best-case scenario is credible in regions where coral reefs are in good health and relatively undamaged from local stressors, e.g., in Palau, where coral reef vertical accretion rates of >10 mm y⁻¹ have been reported (van Woesik et al., 2015). A 'Remain' scenario is based on the fringing coral reef persisting but remaining at the same height. Such a scenario is likely to occur where the aragonite saturation state remains near 3.3; at or below this level it is found that accretion of coral reefs ceases or becomes negative (Kleypas et al., 1999; Hoegh-Guldberg et al., 2007). The third, most extreme, fringing reef scenario is if the coral reef 'Gives-up' and disappears. The 'Give-up' scenario is already happening in regions around the world where coral reefs experience intense local stressors, in addition to climate change (Hughes, 1994; Hoegh-Guldberg et al., 2007). Because seagrass meadows in tropical bays and lagoons are largely dependent on the sheltered conditions within the shadow of fringing coral reefs, it logically follows that declines in coral reefs will be matched by a decline in seagrass meadows, as was shown in modelling studies (Saunders et al., 2014; Keyzer et al., 2020).

Sea level predictions for coastlines around the globe show variations of a rise between 0.11 and 0.33 m for 2 °C of warming and 0.54 to 1.08 m for 5 °C of warming by the end of the century (Jevrejeva et al., 2016). Such a rise in the sea level constitutes a significant increase in the relative depth within the nearshore region, and will result in larger waves reaching closer to shore (Quataert et al., 2015; Keyzer et al., 2020; Zhu et al., 2020). Keyzer et al. (2020) displayed how the height of the fringing coral reef has the largest effect on the orbital flow velocity and flow speed within tropical bays. In a bay that loses its fringing coral reef and experiences a sea level rise of 0.87 m (sea-level rise predicted in the Caribbean for 2100 by

Jevrejeva et al. (2016)), the spatially-average orbital velocity increases by 23 % (Supplementary 1, Keyzer et al., 2020). Even if the reef remains, there is a 11 % increase in the orbital flow velocity across the bay (Supplementary 1, Keyzer et al., 2020). This increase in hydrodynamic energy within the bay is exacerbated when seagrass vegetation is lost, with there being a further 4-5 % increase in the orbital flow velocity when there is no seagrass (Supplementary 1, Keyzer et al., 2020). Such an increase in sea-level and hydrodynamic forces within the coastal region will fundamentally impact the functioning of coastal ecosystems and the services that they provide.

The sea level in the Caribbean region is projected to rise by 0.87 m by 2100 under a 5 °C temperature increase (Jevrejeva et al., 2016). In addition, much of the Caribbean's natural coral reefs are considered in a degraded state (Jackson et al., 2014). The combination of these two factors could result in a drastic alteration in the Caribbean's bays and lagoons over the next 100 years. High-resolution simulations of how the hydrodynamic forces within a natural Caribbean seagrass-vegetated bay may change in the future, given sea-level rise and potential scenarios of coral reef and seagrass degradation (Coral reefs 'keep up', 'remain' or 'disappear', and seagrass remains or disappears) were conducted by Keyzer et al. (2020). Combining

these hydrodynamic simulations with a mechanistic understanding of the coastal protection and unique chemical habitat services provided by seagrass meadows, we spatially model how the physical and chemical feedbacks associated with coral reef-seagrass ecosystems will be impacted by sea level rise and ecosystem degradation. High spatial and temporal resolution measurements were required to quantify the seagrass ecosystem services and their provision in a natural setting, thus, the spatial model in this study was applied to a single bay. Because we have done a mechanistic study, the relative trends shown here are applicable to all tropical seagrass-fringing reef habitats. The results from this study display how the ecosystem services provided by seagrass meadows will change with sea-level rise and the effect that this has on the physical and chemical environment within tropical bays.

2. Materials and methods

2.1. Site description

Baie de L'Embouchure, a seagrass-dominated bay on the eastern coast of St Martin, Caribbean (Fig. 1a, b) was used to explore how the pH alteration,

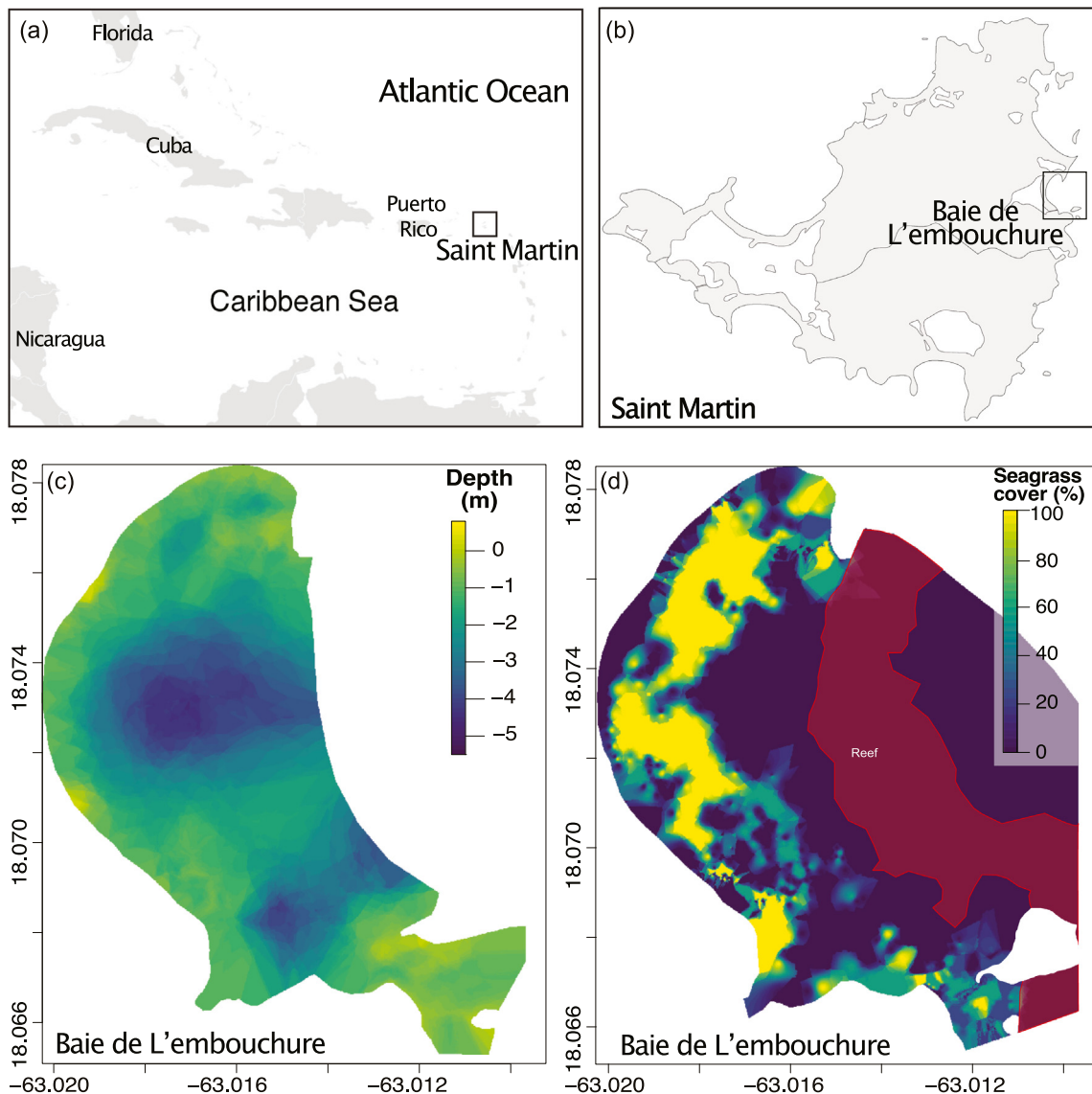


Fig. 1. Map showing Saint Martin, which is situated in the Caribbean Sea (a), with the study site Baie de L'embouchure highlighted in (b). The bathymetry (c) and seagrass coverage (percent benthic cover, d) across Baie de L'Embouchure are shown below, with the fringing reef highlighted in red.

wave attenuation and sediment stabilisation services provided by seagrass meadows and fringing coral reefs will be affected by sea level rise. This bay was chosen due to its relatively pristine condition and extensive seagrass meadow. St Martin is part of the Caribbean leeward islands, with the eastern side being directly exposed to the swell and trade winds from the Atlantic Ocean. A fringing coral reef protects Baie de L'Embouchure from the largest swell from the Atlantic, creating a sheltered, shallow (up to 5 m; Fig. 1c) environment. Baie de L'Embouchure typically experiences a small tidal range of 0.2–0.3 m, and there are no freshwater inputs. Extensive seagrass meadows, dominated by the late-successional species *Thalassia testudinum*, grow on calcareous sediment throughout the bay. The sediment within the bay is composed of $94 \pm 0.9\%$ ($\pm 95\%$ confidence interval, $n = 25$) CaCO_3 , with $0.4 \pm 0.03\%$ organic carbon. The sediment can be considered unconsolidated coarse sandy sediment, with 90% of the grains measuring above $652 \pm 110 \mu\text{m}$ ($n = 16$), a silt content ($<63 \mu\text{m}$ grain size) of $1.3 \pm 0.9\%$ ($n = 16$) and a dry bulk density of $1.3 \pm 0.08 \text{ g cm}^{-3}$. The calcareous sand is supplied by the erosion of the fringing coral reef and calcifying algae, which grow adjacent to and among the seagrass meadow. The present-day mean pH_T within the bay is 8.14 ± 0.01 (James et al., 2019a).

2.2. Seagrass coverage

Seagrass coverage within Baie de L'Embouchure was mapped by a broad survey where a grid of 1585 spatial points across the bay were defined as unvegetated (0% seagrass coverage), sparse (25% seagrass coverage), medium (50% seagrass coverage) or dense (100% seagrass coverage). An interpolation map depicting the seagrass cover was created using the inverse distance weighting method, where a maximum of 5 neighbouring observations were used to interpolate the known spatial points across the map of Baie de L'Embouchure (Fig. 1d). R version 3.3 (R Core Team, 2017) and the packages CRAN:sp (Pebesma and Bivand, 2005; Bivand et al., 2013), CRAN:rgdal (Bivand et al., 2016), CRAN:'dismo' (Hijmans et al., 2011) and CRAN:gstat (Pebesma, 2004) were used to create the interpolation maps.

2.3. Hydrodynamic model summary

A depth-averaged hydrodynamic model of Baie de L'Embouchure was produced by Keyzer et al. (2020), based on the bathymetry of the bay and the fringing reef. Using Delft3D Flexible Mesh, this model simulates the present-day flow and waves within Baie de L'Embouchure that are driven by oceanic and meteorological forcings. The D-Waves (Deltares, 2018), D-Flow (Deltares, 2018) and vegetation modules (Deltares, 2018) were included in the model, so that the flow, waves, their mutual interactions and their interaction with vegetation were all included in the simulations. An extensive description of the equations and specific model can be found in (Kernkamp et al., 2011; Keyzer, 2018). This model was validated against in situ wave measurements taken from within Baie de L'embouchure and show good agreement (Supplementary 2). The time-averaged orbital flow velocities and flow speeds produced by the hydrodynamic model were used for this study.

2.4. Future hydrodynamic scenarios

A sea level 0.87 m above present-day was used for the future scenarios, representing the sea level rise predicted for the Caribbean region by 2100 based on the IPCC's RCP8.5 scenario (Jevrejeva et al., 2016). In addition to the sea level rise, varying scenarios simulating different responses of the fringing coral reef and seagrass meadows to global change were also conducted (Fig. 2). Three scenarios for the coral reef were considered by altering the bathymetry within the hydrodynamic model: (1) Keep-up: coral reef growth rate keeps up with sea level rise, (2) Remain: coral reef survives but stays the same height as present-day, and (3) Give-up: the coral reef dies and the fringing reef structure is removed from the bathymetry. Within each of these coral reef scenarios, simulations with present day seagrass

coverage being (a) present or (b) absent were conducted by turning the vegetation module on or off in the Delft3D model. All seagrass scenarios were considered, except the absence of seagrass when the coral reef keeps up as it would be assumed the conditions would remain favourable for seagrass under this scenario (Fig. 2).

2.5. Measurements of ecosystem services

2.5.1. Grain size

Sediment grain size distribution is dependent upon the sediment source and the bottom shear stress, with finer grains settling in areas where the bottom shear stress is reduced (Shields, 1936). The sediment within Baie de L'Embouchure is coarse grain sand, composed of 95% CaCO_3 . Due to the majority of the sediment originating from the fringing coral reef and the calcareous algae growing within Baie de L'Embouchure, the sediment supply should be relatively uniform across the bay, therefore, the bottom shear stress is assumed to be the main driver of sediment grain size variability across the bay. The flow regime, depth and density of vegetation significantly impact the bottom shear stress and were used to assess the variability of grain size within Baie de L'Embouchure. To derive an estimate of the effect of seagrass, water depth and water flow on the sediment grain size, sediment samples were collected in 50 mL sampling containers from unvegetated areas and in seagrass patches (patches $> 2 \text{ m}^2$) across Baie de L'Embouchure. Seagrass coverage and GPS position were recorded for each sampling position. The sediment samples were taken in haphazardly chosen locations in the northern, north-eastern, eastern, south-eastern, southern and middle of the bay. The sediment samples were freeze-dried and sieved through a one mm sieve. Sediment larger than one mm was manually weighed to determine its proportion, while the remaining sediment grain size distribution was measured by laser diffraction on a Malvern Mastersizer 2000 (McCave et al., 1986). A correlation between the flow speed, orbital velocity and seagrass coverage at the collected locations with the measured grain size was identified, as described in detail below.

2.5.2. Sediment erosion threshold

To derive a relationship between seagrass coverage, grain size and the sediment erosion threshold, data on the stability of sediment in unvegetated and seagrass-vegetated patches was obtained from James et al. (2019b). This study measured the sediment erosion threshold (flow at which sediment began to move) within unvegetated areas, patches of 50% *T. testudinum* and patches of 100% *T. testudinum* in Baie de L'Embouchure. The erosion thresholds were directly measured in situ with the TiDyFLOW flume. The TiDyFLOW flume is a portable flume in which a unidirectional flow can be controlled up to speeds up to 1 m s^{-1} , allowing for direct erosion threshold measurements on natural seagrass meadows. Grain size distribution was measured within each replicated patch, to account for differences in the grain size between vegetation patches and the easier movement of smaller particles (Shields, 1936).

2.5.3. pH variable habitat

Data on the influence that varying levels of seagrass coverage have on the magnitude of diurnal pH fluctuations observed within *T. testudinum* meadows were obtained from James et al. (2019a). This data monitored the diurnal pH variability within and outside of seagrass meadows of *T. testudinum* at a sheltered seagrass meadow in the northern end of Baie de L'Embouchure, at a strong unidirectional flow site in the southern end of Baie de L'Embouchure, and at an exposed site in the neighbouring Orient Bay of St Martin. Measurements from multiple sites with varying hydrodynamic regimes, ensured that the pH measurements covered a wide distribution of hydrodynamic conditions and seagrass coverage. The pH fluctuations i.e. the magnitude that the pH fluctuates from day to night within an area of seagrass was used as a proxy for the provision of a unique pH habitat within the vegetated bay.

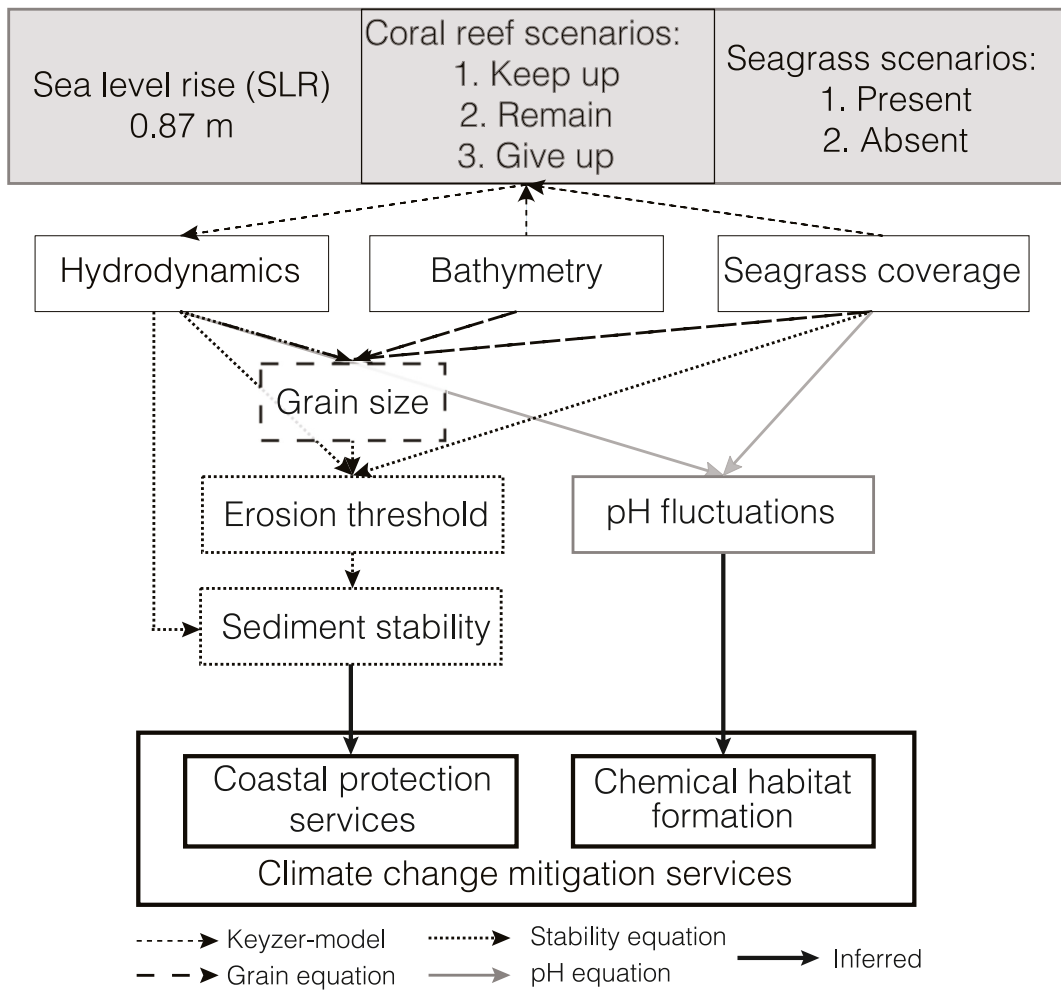


Fig. 2. The method process depicting the future scenarios used for the hydrodynamic simulation and the variables used for predicting the environmental parameters and ecosystem services. Simulations (Grey boxes) of hydrodynamic conditions now and in the future from the Keyzer-model were used alongside field measurements (open “white” boxes) of how seagrass coverage affects: pH variability, grain size and sediment erosion thresholds.

2.6. Predicting spatial coverage of ecosystem services within a vegetated bay

2.6.1. Statistical models

Using regression analysis, statistical models were created to predict the spatial variation in the diurnal pH fluctuations, the median sediment grain size and the sediment erosion threshold across Baie de L'Embouchure. The regression analyses were created using the existing published data from Baie de L'Embouchure and neighbouring sites on St Martin (described above). These field measurements were calibrated against the hydrodynamic model, by determining the depth-averaged orbital flow velocity and flow speed from the hydrodynamic model at each of the pH and grain size measurement locations.

2.6.2. Grain size prediction

A linear regression was used to predict the median grain size, based on the grain size dataset detailed above. Seagrass coverage (measured), depth (measured), orbital flow velocity (modelled), flow speed (modelled), and all interactions were used as continuous predictor variables. The model of best fit was selected based on the AIC criterion and resulted in the equation:

$$\text{Median grain size} = \text{Seagrass cover} + \text{Orbital velocity} + \text{Flow speed} + \text{Depth} + \text{Seagrass cover} \times \text{Depth} \quad (1)$$

Where \times denotes an interaction term between the two factors. As this was a linear model, a bottom limit of 1 μm was set to ensure no negative grain size predictions.

2.6.3. Sediment stability

Median grain size (measured) and seagrass coverage (measured) and their interaction were used as predictor variables in a regression analysis to predict the sediment erosion threshold.

$$\text{Erosion threshold} = \text{Seagrass cover} + \text{Median grain size} + \text{Seagrass cover} \times \text{Median Grain size} \quad (2)$$

Sediment stability was calculated as the percent difference between the predicted erosion threshold and the maximum hydrodynamic force (either flow speed or orbital velocity) at each spatial point. Thereby, a sediment stability of 0 represents that the maximum flow is equal to the calculated erosion threshold (Eq. (2)), below 0 indicates that the flow exceeds that of the calculated erosion threshold so that sediment is likely to erode, and above 0 indicates that the calculated erosion threshold is above that of the maximum flow so that the sediment is stable. Because the sediment stability measurements were conducted under unidirectional flow, it is expected that our predictions will be conservative in areas where orbital motion is the predominant hydrodynamic force. Orbital forces create more turbulence at the seafloor, and thereby cause sediment to move at slower velocities compared to unidirectional flow (James et al., 2020a).

2.6.4. pH variable habitat prediction

pH variability is driven by the photosynthesising vegetation and is counteracted by hydrodynamic forces. To create a prediction of the pH variability across the vegetated Baie de L'Embouchure, a combined logistic and

linear regression approach was utilised. Firstly, the probability of seagrass occurrence was statistically modelled with logistic regression, using the presence/absence data from the seagrass survey dataset combined with the hydrodynamic parameters at each spatial point from the Keyzer model (Keyzer et al., 2020). Based on the Akaike Information Criterion (AIC) criterion, the following factors were included: water depth (linear and squared), orbital velocity (linear and squared), flow speed (linear and squared) and the interaction between these factors. This resulted in the statistical model:

$$P_{sg} = \text{Orbital velocity}^2 + \text{Flow speed} + \text{Depth}^2 \quad (3)$$

Where P_{sg} is the probability of seagrass occurring. Secondly, the effect size that seagrass density has on the diurnal pH fluctuations was estimated from the pH variability dataset (detailed above), by creating a linear regression, giving the model:

$$\text{Seagrass effect on pH} = \text{Seagrass cover} \quad (4)$$

Finally, the logistic and linear regression models were combined to give a statistical model that predicts the magnitude of the diurnal pH fluctuations:

$$\text{pH fluctuations} = P_{sg} + \text{Seagrass effect on pH} + P_{sg} \times \text{Seagrass effect on pH} \quad (5)$$

Statistical modelling was conducted with R version 3.3 (R Core Team, 2017) and the CRAN:MASS package (Venables and Ripley, 2002). Factors in the model were tested for multicollinearity and the linear regression models were additionally tested for homoscedasticity and normality. All models passed these assumptions. The fit of the regression models are illustrated in Fig. 3.

2.6.5. Spatial coverage of ecosystem services

The hydrodynamic model was used to determine the orbital flow velocity, flow speed and depth at each spatial point where the seagrass coverage survey was conducted (1585 points in total) for the present-day and future hydrodynamic scenarios. For each of these spatial points, the predictive equations from the regression analyses were applied to predict the median sediment grain size, the sediment stability and the magnitude of the diurnal pH fluctuations under present-day and future hydrodynamic conditions within Baie de L'Embouchure. Interpolation maps were created to map the median grain size, sediment stability and pH variability across Baie de L'Embouchure, using the inverse distance weighting method and the same packages described above for interpolating seagrass coverage. Coastline retreat and changes in seagrass coverage (other than presence/absence) were not included in our model, with this study focussing on the change in the extent of present-day ecosystem services.

3. Results

3.1. Sensitivity of coastal protection services to sea level rise

Sediment size increases with increasing hydrodynamic forces, however, decreases with increasing seagrass coverage and depth (Supplementary 3). Greater hydrodynamic forces entering a bay under future sea-level scenarios only result in an increase in the average median sediment grain size when the seagrass is also lost (Fig. 4). In the absence of seagrass (scenarios F3 & F5), the average median grain size increases by 6-7 % from 502 ± 5.6 (95 % CI) in present day conditions up to 583 ± 5.5 when both the seagrass and fringing reef are lost (Fig. 4).

3.2. Sediment stability

Using the present-day seagrass coverage and predicted median grain size and hydrodynamic conditions, we estimated the stability of the sediment within a bay in the future. The present-day sediment within the studied bay is coarse calcareous sand with a bay-averaged median grain size of

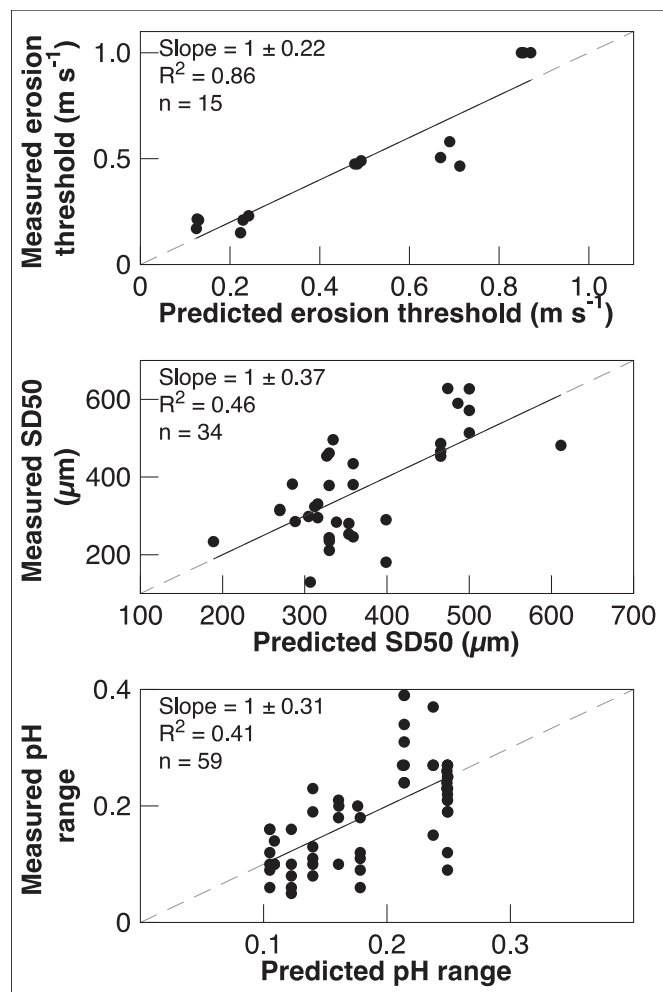


Fig. 3. Illustration of fit of the prediction equations for the 3 aspects of seagrass ecosystem services: sediment erosion threshold, sediment grain size and pH habitat. Figures display the measured data plotted against the predicted values. Solid line indicates the linear regression with the slope \pm 95 % CI, R^2 and n detailed on each plot.

$332.3 \pm 44.3 \mu\text{m}$ ($n = 16$), however, the relatively low bulk density (dry bulk density = $1.3 \pm 0.08 \text{ g cm}^{-3}$, $n = 16$) means that the drag and lift forces from waves and currents can penetrate the upper sediment surface and cause sediment transport. Seagrass meadows significantly stabilise the sediment surface ($t = 3.696$, $df = 11$, $p < 0.01$; Supplementary 3), ensuring most of the sediment area is stable under future scenarios where seagrass is present (Fig. 4). Under present-day conditions, it is estimated that sediment within 81 % of the area of Baie de L'embouchure is stable under normal conditions i.e. percent sediment stability is >0 % (Fig. 5). The area in which sediment is stable drops to 70 % in the future scenario where seagrass is present and the fringing reef disappears (scenario F4). When seagrass disappears and a low fringing reef remains (scenario F3), only 50 % of the area in the bay is estimated to have stable sediment (Fig. 5). In the worst-case scenario where seagrass and the fringing reef disappears (scenario F5), only 26 % of the bay area has a stable sediment surface, with 74 % of the sediment moving at hydrodynamic forces 50-75 % lower than what was modelled under average flow conditions (Fig. 5).

3.3. Future of pH variable habitat with sea level rise

Photosynthesis and respiration by the seagrass meadow that extends across the bay is estimated to result in 35 % of the bay area experiencing diurnal pH fluctuations ranging above 0.2 units in average present-day hydrodynamic conditions (Fig. 5). Hydrodynamic forces counteract the pH

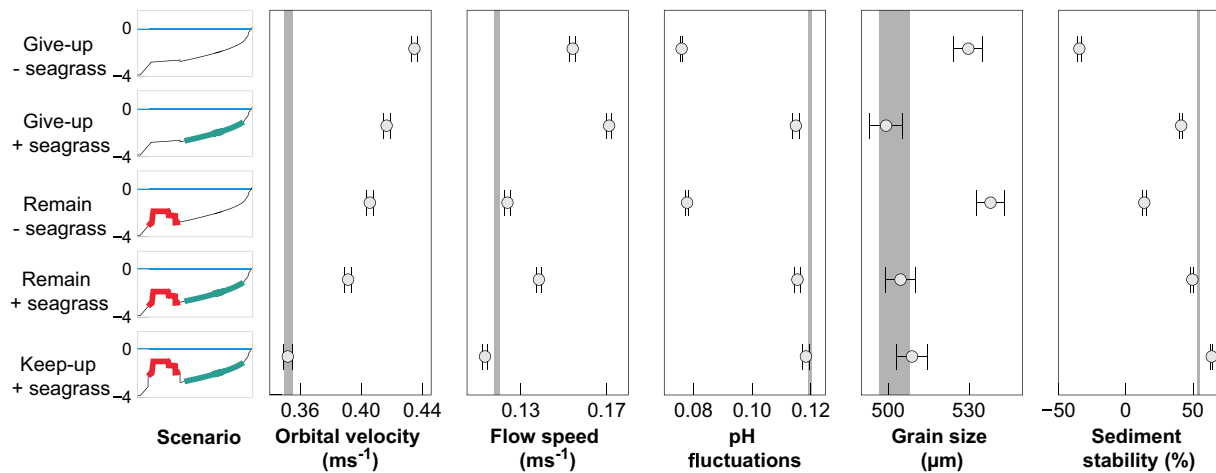


Fig. 4. Spatially-average values across Baie de L'Embouchure of the modelled hydrodynamic forces (depth-averaged orbital velocity and flow speed) and the predicted ecosystem parameters (magnitude of diurnal pH fluctuations, grain size and sediment stability) under the varying future scenarios of sea level rise. Average present-day conditions are represented by the grey shaded area within the graphs. Depth profiles on the left illustrate the depth profiles of the scenarios: red lines indicate the position of the fringing coral reef and green lines indicate the presence of seagrass. Error bars are calculated 95 % confidence intervals ($n = 15,899$).

fluctuations caused by photosynthesis, however, although there is an overall increase in the average hydrodynamic forces with a rise in the sea-level, the deepening of the bay reduces the effects of these greater hydrodynamic forces on the benthic seagrass meadows and the pH variability they create (Fig. 4). When the seagrass meadows remain, the spatial area in which the pH fluctuates diurnally by >0.2 units does not change significantly (Fig. 5). Loss of seagrass, however, is associated with a complete loss of the bay's large pH variability, with the pH of the seawater within the bay reflecting that of the incoming seawater (Fig. 5).

4. Discussion

4.1. Reduction in the ecosystem services magnitude and extent

A fringing coral reef provides an effective wave barrier that shelters adjacent bays and seagrass meadows from strong hydrodynamic forces (Saunders et al., 2014; Keyzer et al., 2020). Even if the vertical accretion of fringing reefs does not keep up with sea level rise, the protection provided by fringing reefs allows the seagrass meadow ecosystem services of coastal protection and chemical habitat formation to persist. The loss of a fringing reef, however, results in greater hydrodynamic forces entering the adjacent bays. Due to an increase in the relative depth caused by sea-level rise, the effect of the increase in hydrodynamic forces on the ecosystem services is partially counteracted and the bed shear stress would be reduced in some areas (Shields, 1936). In the case of Baie de L'embouchure, an increase in hydrodynamic forces increases the overall seafloor area vulnerable to erosion by 10 % when seagrass is still present, although some of the shallower areas actually increase in stability due to becoming deeper. If seagrass is completely lost, however, there is a complete shift in the physical and chemical environment within the bay system. With no seagrass, bay systems will become dominated by a larger grain size in addition to there being no dynamic chemical habitat caused by the fluctuating pH conditions resulting from the seagrass metabolism. These changes in the physical and chemical environment highlight the large effect that seagrass meadows have on tropical bay systems, in particular, their provision of a habitat in which many other organisms are dependent upon.

4.2. Positive feedback of sediment instability

An increase in sediment instability has the potential to create a positive feedback of further sediment instability (van der Heide et al., 2010, 2011;

James et al., 2019b). Greater sediment instability increases turbidity and the likelihood of mechanical damage, burial and uprooting of benthic species (van der Heide et al., 2007, 2011), which can inhibit the growth and colonisation of seagrasses (Williams, 1990; Fonseca and Bell, 1998; Suykerbuyk et al., 2016). As the area of unstable sediment increases, the seagrass meadow can become more fragmented and less able to recover from further disturbance, reducing the resilience of the ecosystem (van der Heide et al., 2007, 2011). Tropical seagrass meadows across the globe are already under threat from eutrophication, land-use changes, physical disturbance and warming (Orth et al., 2006; Waycott et al., 2009). Rates of decline of 7 % yr^{-1} have been estimated for global seagrass meadows, with 58 % of monitored seagrass meadows exhibiting declines (Waycott et al., 2009). Given that the causes of decline are often local disturbance events brought about by human activity, it is difficult to reliably predict future seagrass coverage in the full context of global change. We therefore only examined scenarios of present day coverage and complete absence of seagrass in this study. However, given the positive feedbacks associated with sediment instability in seagrass meadows, any decline in seagrass coverage risks inducing feedbacks that could not only result in the loss of primary productivity and biodiversity (Nagelkerken, 2009; McLeod et al., 2011) but, as we show, would cause widespread erosion and alter the natural and dynamic chemical habitat within tropical bays.

4.3. Loss of ecosystem services exacerbates negative climate change effects

Future scenarios where seagrass is absent display how an unvegetated bay leaves the sediment surface vulnerable to erosion (Ward et al., 1984; Keyzer et al., 2020), as can be seen by the shift to a larger grain size and a larger area with unstable sediment in Baie de L'embouchure (Fig. 5). This increase in sediment instability can exacerbate sea level rise by causing a further deepening of the bay and by reducing the amount of wave attenuation occurring within the subtidal region, which ultimately increases the vulnerability of the surrounding shoreline to erosion and coastal flooding (Quataert et al., 2015; Siegle and Costa, 2017; James et al., 2019b, 2020b; Venancio et al., 2020). Furthermore, an unstable sediment surface is likely to be uninhabitable for many currently existing benthic species within natural tropical bays, such as calcifying algae, urchins and juvenile lobster (Lozano-Álvarez et al., 2009). The benthic community has been shown to be tightly linked to the presence or absence of seagrass (Lundquist et al., 2018; Seitz and Ewers Lewis, 2018; Cadier and Frouws, 2019; Githaiga et al., 2019). Once seagrass is lost, the community assemblage often shifts toward bioturbating organisms that can further hinder

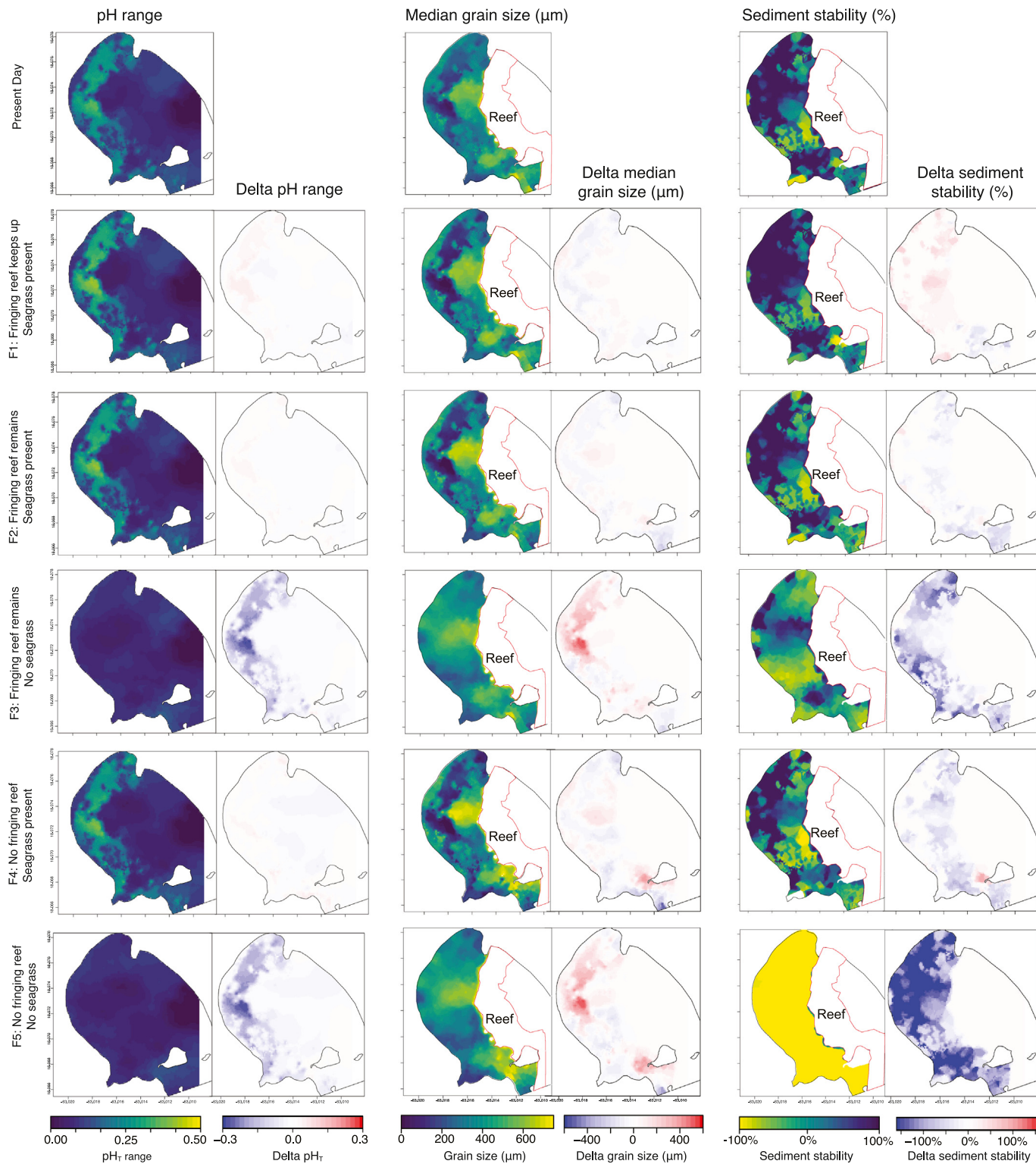


Fig. 5. Interpolation maps display the spatial variability of the magnitude of the diurnal pH fluctuations (pH units), median grain size (μm) and sediment stability (% difference between the sediment erosion threshold and the maximum flow; stable sediment >0 %, unstable sediment <0 %) within Baie de L'Embouchure under the varying future scenarios. The delta maps (light blue and red shading) display the difference compared to the present-day values.

seagrass reestablishment (Cadier and Frouws, 2019). Such a community shift would have significant consequences for the local small-scale fisheries that exist throughout tropical regions and could potentially impact larger fisheries which depend upon seagrass meadows for nursery habitat (Unsworth et al., 2019).

In addition to the physical alterations to the seafloor, the loss of seagrass meadows would result in the loss of the unique chemical habitat within tropical bays. Smaller pH fluctuations within the bay ecosystem exposes vulnerable organisms to the constant low pH, low aragonite state seawater of the open ocean (Pörtner et al., 2014), potentially leading to further losses

in biodiversity (Wootton et al., 2008; Goldenberg et al., 2017). Although the full effect of pH fluctuations on organisms remains unclear (Cornwall et al., 2013; Hurd, 2015; Mangan et al., 2017), the natural spatial and temporal pH variability within vegetated ecosystems is likely to have an indirect effect by increasing the habitat complexity and potentially promoting organisms to acclimate and adapt to variable pH conditions (Botero et al., 2015; Boyd et al., 2016; Rilov et al., 2019). Multi-generational studies have shown how adult populations of mussels and oysters from sites with naturally varying-pH are more resilient to low pH conditions than those from sites exhibiting a stable pH (Parker et al., 2012; Thomsen et al., 2017). Therefore, a complex ecosystem with dynamic conditions is more likely to produce organisms tolerant of changes in their environment, compared to habitats with stable and uniform conditions.

4.4. Other factors affecting provision of ecosystem services

This study examined the effects of future sea-level rise and presence or loss of coral reefs and seagrass meadows on the provision of sediment stabilisation and chemical habitat formation ecosystem services. Global change, however, constitutes a large array of factors that could influence the provision of ecosystem services within seagrass meadows. Examining the loss of the coral reefs and seagrass meadows helps us to see the total effect of these habitats regardless of the factor that may cause such degradation, i.e. physical disturbance from storms, warming, ocean acidification. There are intermediary steps that would occur before complete degradation, however, which would result in less drastic changes to the ecosystem services provided within these habitats. Extreme high temperatures during oceanic heat-wave events can negatively impact the metabolic rates of corals and seagrasses (Hughes and Connell, 1999; Hughes et al., 2017b; Ruthrof et al., 2018), which would increase respiration and thus reduce the chemical habitat formation service, although *Thalassia testudinum* and other late-successional seagrass species have been shown to be resilient of high temperatures (Barber and Behren, 1985; Strydom et al., 2020). Frequent local disturbance events caused by physical damage or eutrophication can facilitate the replacement of late-successional seagrass species, such as *Thalassia testudinum*, by earlier successional species, such as *Syringodium filiforme*, *Halodule wrightii* and the invasive seagrass *Halophila stipulacea*, which are able to tolerate dynamic conditions by growing quickly. These early-successional seagrasses can still provide sediment stabilisation and chemical habitat formation services during calm periods (Christianen et al., 2013; James et al., 2020a). However, they are easily uprooted during extreme hydrodynamic force events (i.e. hurricanes and storms), and thus, would not provide long-term coastal protection services, particularly during storms when these services are most needed (James et al., 2020b, a). And once uprooted, all other seagrass ecosystem services would disappear until re-colonisation, starting at a minimum of 2 months after the disturbance (Willette et al., 2020).

4.5. Conclusions

The sediment stabilisation and chemical habitat formation services provided by tropical seagrass meadows provide a distinct habitat that locally mitigates coastal erosion and supports a wide range of plant and animal species. Sea-level rise threatens the provision of these services by increasing the water depth and consequently, the hydrodynamic forces within the coastal region. These greater hydrodynamic forces limit both the spatial extent and magnitude that the services of sediment stabilisation and chemical habitat formation are provided. Future scenarios of sea-level rise and habitat degradation with hydrodynamic and empirical models show that the presence of a fringing coral reef across a bay helps to maintain these ecosystem services under future sea-level rise, however, when the fringing reef disappears the magnitude of the services are reduced. Degradation of the seagrass meadow itself, however, constitutes the largest risk to the ecosystem. Complete seagrass loss results in a larger sediment grain size that is more unstable in combination with the loss of the diverse and dynamic pH regime. A reduction or loss of the sediment stabilisation and chemical

habitat formation services provided by seagrass meadows will greatly exacerbate the risk of coastal regions to both coastal erosion, flooding and ocean acidification and could lead to community shifts. Maintaining tropical shorelines will become more difficult as the ecosystem services provided by seagrass meadows and coral reefs get overwhelmed by sea level rise. Preventing further declines in coastal ecosystems is essential if we wish to benefit from the natural climate-change mitigation that they provide, and thereby, buffer coastal regions from the substantial risks and costs associated with sea level rise.

Data availability

Data will be made available on request.

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.

Acknowledgments

Permits for the work in St Martin were obtained from the Reserve Naturelle Saint Martin, and we are grateful for their advice and allowing us to conduct our research there.

Funding

This work was supported by NWO 'Caribbean Research: a Multidisciplinary Approach' grant, which was awarded to the SCENES project (Grant number 858.14.063). SJV is supported by the Belgian Federal Science Policy Office (grant no. FED-tWIN2019-prf-008).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159576>.

References

- Anthony, K.R.N., Kline, D.I., Diaz-Pulido, G., Dove, S., Hoegh-Guldberg, O., 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc. Natl. Acad. Sci.* 105, 17442–17446. <https://doi.org/10.1073/pnas.0804478105>.
- Anthony, K.R.N., Kleyvas, J.A., Gattuso, J.-P., 2011. Coral reefs modify their seawater carbon chemistry - implications for impacts of ocean acidification. *Glob. Chang. Biol.* 17, 3655–3666. <https://doi.org/10.1111/j.1365-2486.2011.02510.x>.
- Arkema, K.K., Guannel, G., Verutes, G., et al., 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nat. Clim. Chang.* 3, 913–918. <https://doi.org/10.1038/nclimate1944>.
- Barber, B.J., Behren, P.J., 1985. Effects of elevated temperature on seasonal in situ leaf productivity of *Thalassia testudinum* banks ex König and *Syringodium filiforme* Kützinger. *Aquat. Bot.* 22, 61–69.
- Bivand, R.S., Pebesma, E., Gómez-Rubio, V., 2013. *Applied Spatial Data Analysis with R*. Second edition. Springer, NY.
- Bivand, R., Keitt, T., Rowlingson, B., 2016. Package "rgdal". R Package. <https://doi.org/10.1353/lib.0.0050>.
- Botero, C.A., Weissing, F.J., Wright, J., Rubenstein, D.R., 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proc. Natl. Acad. Sci.* 112. <https://doi.org/10.1073/pnas.1408589111>.
- Boyd, P.W., Cornwall, C.E., Davison, A., Doney, S.C., Fourquez, M., Hurd, C.L., Lima, I.D., McMin, A., 2016. Biological responses to environmental heterogeneity under future ocean conditions. *Glob. Chang. Biol.* 22, 2633–2650. <https://doi.org/10.1111/gcb.13287>.
- Britton, D., Cornwall, C.E., Revill, A.T., Hurd, C.L.C.L., Johnson, C.R., 2016. Ocean acidification reverses the positive effects of seawater pH fluctuations on growth and photosynthesis of the habitat-forming kelp, *Ecklonia radiata*. *Sci. Rep.* 6, 1–10. <https://doi.org/10.1038/srep26036>.
- Burke, L., Reyta, K., Spalding, M., Perry, A., 2011. *Reefs at Risk Revisited*.
- Cadier, C., Frouws, A., 2019. Experimental harvest in a tropical seagrass meadow leads to shift in associated benthic communities. *Community Ecol.* 20, 138–148. <https://doi.org/10.1556/168.2019.20.2.4>.

- 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>.
- Cornwall, C.E., Hepburn, C.D., McGraw, C.M., Currie, K.L., Pilditch, C.A., Hunter, K.A., Boyd, P.W., Hurd, C.L., 2013. Diurnal fluctuations in seawater pH influence the response of a calcifying macroalga to ocean acidification. *Proc. R. Soc.* 280. <https://doi.org/10.1098/rspb.2013.2201>.
- Deltares, 2018. *D-Flow Flexible Mesh User Manual*.
- 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>.
- Falkenberg, L.J., Scanes, E., Ducker, J., Ross, P.M., 2021. Biotic habitats as refugia under ocean acidification. *Conserv. Physiol.* 9, 1–16. <https://doi.org/10.1093/conphys/coab077>.
- Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes. *Mar. Ecol. Prog. Ser.* 171, 109–121.
- Frieder, C.A., Gonzalez, J.P., Bockmon, E.E., Navarro, M.O., Levin, L.A., 2014. Can variable pH and low oxygen moderate ocean acidification outcomes for mussel larvae? *Glob. Chang. Biol.* 20, 754–764. <https://doi.org/10.1111/gcb.12485>.
- Githaiga, M.N., Frouws, A.M., Kairo, J.G., Huxham, M., 2019. Seagrass removal leads to rapid changes in fauna and loss of carbon. *Front. Ecol. Evol.* 7, 1–12. <https://doi.org/10.3389/fevo.2019.00062>.
- Goldenberg, S.U., Nagelkerken, I., Ferreira, C.M., Ullah, H., Connell, S.D., 2017. Boosted food web productivity through ocean acidification collapses under warming. *Glob. Chang. Biol.* 23, 4177–4184. <https://doi.org/10.1111/gcb.13699>.
- Hendriks, I.E., Olsen, Y.S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T.S., Howard, J., Duarte, C.M., 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences* 11, 333–346. <https://doi.org/10.5194/bg-11-333-2014>.
- Hijmans, R.J., Phillips, S., Leathwick, J.R., Elith, J., 2011. *Package 'dismo'*. October.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., et al., 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742. <https://doi.org/10.1126/science.1152509>.
- 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>.
- Hughes, T.P., Connell, J.H., 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnol. Oceanogr.* 44, 932–940. https://doi.org/10.4319/lo.1999.44.3part_2.0932.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., et al., 2017a. Coral reefs in the anthropocene. *Nature* 546, 82–90. <https://doi.org/10.1038/nature22901>.
- Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., et al., 2017b. Global warming and recurrent mass bleaching of corals. *Nature* <https://doi.org/10.1038/nature21707>.
- Hurd, C.L., 2015. Slow-flow habitats as refugia for coastal calcifiers from ocean acidification. *J. Phycol.* 51, 599–605. <https://doi.org/10.1111/jpy.12307>.
- Hurd, C.L., Cornwall, C.E., Currie, K., Hepburn, C.D., McGraw, C.M., Hunter, K.A., Boyd, P.W., 2011. Metabolically induced pH fluctuations by some coastal calcifiers exceed projected 22nd century ocean acidification: a mechanism for differential susceptibility? *Glob. Chang. Biol.* 17, 3254–3262. <https://doi.org/10.1111/j.1365-2486.2011.02473.x>.
- Jackson, J.B.C., Donovan, M.K., Cramer, K.L., Lam, W., 2014. *Status and Trends of Caribbean Coral Reefs: 1970-2012*.
- James, R.K., Katwijk, M.M., Tussenbroek, B.I., et al., 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., et al., 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>.
- James, R.K., Christianen, M.J.A., van Katwijk, M.M., de Smit, J.C., Bakker, E.S., van der Heide, T., Herman, P.M.J., Bouma, T.J., 2020a. Seagrass coastal protection services reduced by invasive species expansion and megaherbivore grazing. *J. Ecol.* <https://doi.org/10.1111/1365-2745.13411>.
- James, R.K., Lynch, A., Herman, P.M.J., et al., 2020b. Tropical biogeomorphic seagrass landscapes for coastal protection: persistence and wave attenuation during major storms events. *Ecosystems* <https://doi.org/10.1007/s10021-020-00519-2>.
- Jevrejeva, S., Jackson, L.P., Riva, R.E.M., Grinstead, A., Moore, J.C., 2016. Coastal sea level rise with warming above 2 °C. *Proc. Natl. Acad. Sci.* 113, 13342–13347. <https://doi.org/10.1073/pnas.1605312113>.
- Jokiel, P.L., Rodgers, K.S., Kuffner, I.B., Andersson, A.J., Cox, E.F., Mackenzie, F.T., 2008. Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27, 473–483. <https://doi.org/10.1007/s00338-008-0380-9>.
- Kapsenberg, L., Miglioli, A., Bitter, M.C., Tambuttè, E., Dumollard, R., Gattuso, J.P., 2018. Ocean pH fluctuations affect mussel larvae at key developmental transitions. *Proc. R. Soc. B Biol. Sci.*, 285 <https://doi.org/10.1098/rspb.2018.2381>.
- 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 Dyn.* 61, 1175–1188. <https://doi.org/10.1007/s10236-011-0423-6>.
- Keyzer, L.M., 2018. Predicting the impact of sea-level rise in Baie Orientale and Baie de L'Embouchure, Saint Martin. Delft University of Technology.
- Keyzer, L.M., Herman, P.M.J., Smits, B.P., 2020. The Potential of Coastal Ecosystems to Mitigate the Impact of Sea-level Rise in Shallow Tropical Bays In review.
- Kleypas, J.A., McManu, J.W., Mene, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39, 146–159. <https://doi.org/10.1093/icb/39.1.146>.
- Koweek, D.A., Zimmerman, R.C., Hewett, K.M., et al., 2018. Expected limits on the ocean acidification buffering potential of a temperate seagrass meadow. *Ecol. Appl.* 28, 1694–1714. <https://doi.org/10.1002/eap.1771>.
- Lozano-Álvarez, E., Meiners, C., Briones-Fourzán, P., 2009. Ontogenetic habitat shifts affect performance of artificial shelters for Caribbean spiny lobsters. *Mar. Ecol. Prog. Ser.* 396, 85–97. <https://doi.org/10.3354/meps08306>.
- Lundquist, C.J., Jones, T.C., Parkes, S.M., Bulmer, R.H., 2018. Changes in benthic community structure and sediment characteristics after natural recolonisation of the seagrass *Zostera muelleri*. *Sci. Rep.* 8, 1–9. <https://doi.org/10.1038/s41598-018-31398-2>.
- Mangan, S., Urbina, M.A., Findlay, H.S., Wilson, R.W., Lewis, C., 2017. Fluctuating seawater pH/pCO₂ regimes are more energetically expensive than static pH/pCO₂ levels in the mussel *Mytilus edulis*. *Proc. R. Soc. B Biol. Sci.* 284, 0–7. <https://doi.org/10.1098/rspb.2017.1642>.
- McCave, I.N., Bryant, R.J., Cook, H.F., Coughanowr, C.A., 1986. Evaluation of a laser-diffraction-size analyzer for use with natural sediments. *J. Sediment. Res.* 56, 561–564. <https://doi.org/10.1306/212F89CC-2B24-11D7-8648000102C1865D>.
- McLeod, E., Chmura, G.L., Bouillon, S., et al., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560. <https://doi.org/10.1890/110004>.
- Meehl, G.A., Tebaldi, C., 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305, 994–997. <https://doi.org/10.1126/science.1098704>.
- Morris, R.L., Konlechner, T.M., Ghisalberti, M., Swearer, S.E., 2018. From grey to green: efficacy of eco-engineering solutions for nature-based coastal defence. *Glob. Chang. Biol.* 24, 1827–1842. <https://doi.org/10.1111/gcb.14063>.
- Nagelkerken, I., 2009. Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. *Ecological Connectivity among Tropical Coastal Ecosystems*, pp. 357–399.
- Nagelkerken, I., van der Velde, G., 2003. Connectivity between coastal habitats of two oceanic Caribbean islands as inferred from ontogenetic shifts by coral reef fishes. *Gulf Caribb. Res.* 14, 43–59. <https://doi.org/10.18785/gcr.1402.04>.
- Neumann, A.C., Macintyre, I., 1985. Reef response to sea level rise: Keep-up, catch-up or give up. *Proceedings 5th International Coral Reef Congress, Tahiti*.
- Noisette, F., Pansch, C., Wall, M., Wahl, M., Hurd, C.L., 2022. Role of hydrodynamics in shaping chemical habitats and modulating the responses of coastal benthic systems to ocean global change. *Glob. Chang. Biol.* 0–3. <https://doi.org/10.1111/gcb.16165>.
- Oliver, E.C.J., 2019. Mean warming not variability drives marine heatwave trends. *Clim. Dyn.* 53, 1653–1659. <https://doi.org/10.1007/s00382-019-04707-2>.
- Oliver, E.C.J., Benthuisen, J.A., Darmaraki, S., Donat, M.G., Hobday, A.J., Holbrook, N.J., Schlegel, R.W., Gupta, A.S., 2021. Marine heatwaves. *Annu. Rev. Mar. Sci.* 13, 313–342. <https://doi.org/10.1146/annurev-marine-032720>.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., et al., 2006. A global crisis for seagrass ecosystems. *Bioscience* 56, 987–996. [https://doi.org/10.1641/0006-3568\(2006\)56\[987:agcfsel\]2.0.co;2](https://doi.org/10.1641/0006-3568(2006)56[987:agcfsel]2.0.co;2).
- Pansch, C., Schaub, I., Havenhand, J., Wahl, M., 2014. Habitat traits and food availability determine the response of marine invertebrates to ocean acidification. *Glob. Chang. Biol.* 20, 765–777. <https://doi.org/10.1111/gcb.12478>.
- Parker, L.M., Ross, P.M., O'Connor, W.A., Borysko, L., Raftos, D.A., Pörtner, H.O., 2012. Adult exposure influences offspring response to ocean acidification in oysters. *Glob. Chang. Biol.* 18, 82–92. <https://doi.org/10.1111/j.1365-2486.2011.02520.x>.
- Paul, M., Bouma, T.J., Amos, C.L., 2012. Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. *Mar. Ecol. Prog. Ser.* 444, 31–41. <https://doi.org/10.3354/meps09489>.
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* <https://doi.org/10.1016/j.cageo.2004.03.012>.
- Pebesma, E.J., Bivand, R.S., 2005. *Classes and Methods for Spatial Data in R*. R News, p. 5.
- Pörtner, H.-O., Karl, D.M., Boyd, P.W., Cheung, W.W.L., Lluich-Cota, S.E., Nojiri, Y., Schmidt, D.N., Zavialov, P.O., 2014. Ocean systems. In: Field, C.B., Barros, V.R., Dokken, D.J. (Eds.), *Climate Change 2014 Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, pp. 411–484.
- Potouroglou, M., Bull, J.C., Krauss, K.W., et al., 2017. Measuring the role of seagrasses in regulating sediment surface elevation. *Sci. Rep.* 7, 11917. <https://doi.org/10.1038/s41598-017-12354-y>.
- 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. <https://doi.org/10.1002/2015GL064861>.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*.
- Rilov, G., Mazaris, A.D., Stelzenmüller, V., et al., 2019. Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, ecological and genetic studies? *Glob. Ecol. Conserv.* 17. <https://doi.org/10.1016/j.gecco.2019.e00566>.
- Ruthrof, K.X., Breshears, D.D., Fontaine, J.B., et al., 2018. Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. *Sci. Rep.* 8. <https://doi.org/10.1038/s41598-018-31236-5>.
- Saunders, M.I., Leon, J.X.J., Callaghan, D.P., et al., 2014. Interdependency of tropical marine ecosystems in response to climate change. *Nat. Clim. Chang.* 4, 724–729. <https://doi.org/10.1038/nclimate2274>.
- Seitz, R.D., Ewers Lewis, C.J., 2018. Loss of seagrass results in changes to benthic infaunal community structure and decreased secondary production. *Bull. Mar. Sci.* 94, 1273–1292. <https://doi.org/10.5343/bms.2017.1011>.
- Shields, I.A., 1936. Application of similarity principles and turbulence research to bed-load movement. U.S. Soil Conservation Service Coop. Lab. (Translators)In: Ott, W.P., van Uchelen, J.C. (Eds.), *Hydrodynamics Laboratory Publication*. vol. 167. California Institute of Technology, Pasadena.
- Shields, F.D., Coulton, K.G., Nepf, H., 2017. Representation of vegetation in two-dimensional hydrodynamic models. *J. Hydraul. Eng.* 143, 02517002. [https://doi.org/10.1061/\(ASCE\)HY.1943-7900.0001320](https://doi.org/10.1061/(ASCE)HY.1943-7900.0001320).
- Siegle, E., Costa, M.B., 2017. Nearshore wave power increase on reef-shaped coasts due to sea-level rise. *Earths Future* 5, 1054–1065. <https://doi.org/10.1002/2017EF000624>.
- Smale, D.A., Wernberg, T., Oliver, E.C.J., et al., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang.* 9, 306–312. <https://doi.org/10.1038/s41558-019-0412-1>.

- Storlazzi, C.D., Elias, E., Field, M.E., Presto, M.K., 2011. Numerical modeling of the impact of sea-level rise on fringing coral reef hydrodynamics and sediment transport. *Coral Reefs* 30, 83–96. <https://doi.org/10.1007/s00338-011-0723-9>.
- Strydom, S., Murray, K., Wilson, S., et al., 2020. Too hot to handle: unprecedented seagrass death driven by marine heatwave in a world heritage area. *Glob. Chang. Biol.* 26, 3525–3538. <https://doi.org/10.1111/gcb.15065>.
- Sutton-Grier, A.E., Wowk, K., Bamford, H., 2015. Future of our coasts: the potential for natural and hybrid infrastructure to enhance the resilience of our coastal communities, economies and ecosystems. *Environ. Sci. Pol.* 51, 137–148. <https://doi.org/10.1016/j.envsci.2015.04.006>.
- Suykerbuyk, W., Bouma, T.J., Govers, L.L., Giesen, K., de Jong, D.J., Herman, P., Hendriks, J., van Katwijk, M.M., 2016. Surviving in changing seascapes: sediment dynamics as bottleneck for long-term seagrass presence. *Ecosystems* 19, 296–310. <https://doi.org/10.1007/s10021-015-9932-3>.
- Thomsen, J., Stapp, L.S., Haynert, K., Schade, H., Danelli, M., Lannig, G., Wegner, K.M., Melzner, F., 2017. Naturally acidified habitat selects for ocean acidification-tolerant mussels. *Sci. Adv.* 3, 1–9. <https://doi.org/10.1126/sciadv.1602411>.
- Unsworth, R.K.F., Nordlund, L.M., Cullen-Unsworth, L.C., 2019. Seagrass meadows support global fisheries production. *Conserv. Lett.* 12. <https://doi.org/10.1111/conl.12566>.
- 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., Bouma, T.J., van Nes, E.H., van de Koppel, J., Scheffer, M., Roelofs, J.G.M., van Katwijk, M.M., Smolders, A.J.P., 2010. Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. *Ecology* 91, 362–369. <https://doi.org/10.1890/08-1567.1>.
- 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, 1–7. <https://doi.org/10.1371/journal.pone.0016504>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*.
- Venancio, K.K., Garcia, P.D., Gireli, T.Z., Corrêa, T.B., 2020. Hydrodynamic modeling with scenario approach in the evaluation of dredging impacts on coastal erosion in Santos (Brazil). *Ocean Coast. Manag.* 195. <https://doi.org/10.1016/j.ocecoaman.2020.105227>.
- Wahl, M., Schneider Covachá, S., Saderne, V., Hiebenthal, C., Müller, J.D., Pansch, C., Sawall, Y., 2018. Macroalgae may mitigate ocean acidification effects on mussel calcification by increasing pH and its fluctuations. *Limnol. Oceanogr.* 63, 3–21. <https://doi.org/10.1002/lno.10608>.
- Ward, L.G., M. K. W. Boynton, W.R., 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar. Geol.* 59, 85–103. [https://doi.org/10.1016/0025-3227\(84\)90089-6](https://doi.org/10.1016/0025-3227(84)90089-6).
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci.* 106, 12377–12381. <https://doi.org/10.1073/pnas.0905620106>.
- Willette, D.A., Chiquillo, K.L., Cross, C., Fong, P., Kelley, T., Toline, C.A., Zweng, R., Muthukrishnan, R., 2020. Growth and recovery after small-scale disturbance of a rapidly-expanding invasive seagrass in St. John, U.S. Virgin Islands. *J. Exp. Mar. Biol. Ecol.* 523. <https://doi.org/10.1016/j.jembe.2019.151265>.
- Williams, S.L., 1990. Experimental studies of Caribbean seagrass bed development. *Ecol. Monogr.* 60, 449–469. <https://doi.org/10.2307/1943015>.
- 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. <https://doi.org/10.1098/rsos.150181>.
- Wootton, J.T., Pfister, C.A., Forester, J.D., 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl. Acad. Sci. U. S. A.* 105, 18848–18853. <https://doi.org/10.1073/pnas.0810079105>.
- Zhu, Z., van Belzen, J., Zhu, Q., van de Koppel, J., Bouma, T.J., 2020. Vegetation recovery on neighboring tidal flats forms an Achilles' heel of saltmarsh resilience to sea level rise. *Limnol. Oceanogr.* 65, 51–62. <https://doi.org/10.1002/lno.11249>.