

Regional Assessment of the Seagrass *Thalassia testudinum* Banks & Sol. ex K.D.Koenig in the Tropical Atlantic Seagrass Bioregion (Bioregion 2) for the IUCN Red List ¹

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PLANTAE - TRACHEOPHYTA - LILIOPSIDA - ALISMATALES - HYDROCHARITACEAE - *Thalassia - testudinum*

Common Names: Turtlegrass (English), Species code: Tt (English)

Synonyms: none

Red List Status
NT - Near Threatened, (IUCN version 3.1)
Extent of Occurrence (EOO) in Bioregion 2= 8,418,049 km ²
Area of occupancy (AOO) in Bioregion 2= not determined

Red List Assessment

Assessment Information

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Time period assessed: 2007-2020

Assessment Rationale

Thalassia testudinum is a robust seagrass species forming stable extensive dense seagrass beds and is thought to be the most important habitat-forming seagrass species in the Greater Caribbean (Caribbean, Gulf of Mexico and Bermuda). In areas that are only moderately impacted by humans, this species is relatively resistant to physical disturbance by major storms or hurricanes. However, region-wide localized threats to *T. testudinum* including coastal development,

¹ This regional assessment also constitutes the global assessment for this species, given that its global distribution is limited to the Tropical Atlantic Seagrass Bioregion.

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eutrophication, sedimentation, overgrowth by the non-native seagrass *Halophila stipulacea*, and overgrazing by turtles, have contributed to local declines throughout its entire distribution area. Increasing coastal development has the potential to cause more widespread declines. No region-wide mapping efforts exist, and therefore it is impossible to determine the percentage loss of *T. testudinum* meadows throughout its distribution area, at this time. Presently, this species still forms extensive meadows, and the total loss of seagrass due to above-mentioned factors is not thought to reach 30%. However, the ongoing pressures of developments such as eutrophication and sedimentation, and recurrent chronic and acute disturbances causing ecosystem shifts or mortality, such as the sargassum brown tides and Florida Bay die-offs, are a worrying trend. This is a slow-growing species that requires various decades to develop dense meadows, thus recovery in the case of such ongoing or recurrent threats is unlikely. Since this is the most important habitat-forming species in the Greater Caribbean, and cannot be replaced functionally by another species, its available habitat should be closely monitored. Considering that throughout the region, local declines have been reported since 2007, this species is changing from Least Concern (LC, 2007 assessment) to Near Threatened (NT A2ace+3ce).

Distribution

Geographic Range

Thalassia testudinum is only found in the Tropical Atlantic Seagrass Bioregion. It occurs in the western central Atlantic from Florida, USA to Venezuela, throughout the Gulf of Mexico and the Caribbean Sea. It is also found in Bermuda.

Elevation / Depth / Depth Zones

Depth Lower Limit (in metres below sea level): ~20 m (Duarte, 1991).

Depth Upper Limit (in metres below sea level): 0

Depth Zone: Shallow photic (0-50m); usually between 0-5m depth (Duarte, 1991)

Map Status

Map Status	How the map was created, including data sources/methods used:	Please state reason for map not available:	Data Sensitive?	Justification	Geographic range this applies to:	Date restriction imposed:
Done	EOO only. The extreme distribution points were verified from Juman & Alexander (2006), van Tussenbroek et al. (2014), Congdon & Dunton (2016) and Arrellano-Méndez et al (2019). Other occurrence points defining the EOO polygon were sourced and verified from Seagrass Spotter (https://seagrassspotter.org/sightings/map) and Global Biodiversity Information Facility (https://www.gbif.org)	-	-	-	Bioregion 2	-

Occurrence

Countries of Occurrence ²

Country	Presence	Origin	Formerly Bred	Seasonality
Anguilla	Extant	Native	-	Resident
Antigua and Barbuda	Extant	Native	-	Resident
Aruba	Extant	Native	-	Resident
Bahamas	Extant	Native	-	Resident
Barbados	Extant	Native	-	Resident
Belize	Extant	Native	-	Resident
Bermuda	Extant	Native	-	Resident
Bonaire, Sint Eustatius and Saba	Extant	Native	-	Resident
Bonaire, Sint Eustatius and Saba -> Bonaire	Extant	Native	-	Resident
Bonaire, Sint Eustatius and Saba -> Saba	Extant	Native	-	Resident
Bonaire, Sint Eustatius and Saba -> Sint Eustatius	Extant	Native	-	Resident
Cayman Islands	Extant	Native	-	Resident
Colombia	Extant	Native	-	Resident
Costa Rica	Extant	Native	-	Resident
Cuba	Extant	Native	-	Resident
Curaçao	Extant	Native	-	Resident
Dominica	Extant	Native	-	Resident
Dominican Republic	Extant	Native	-	Resident
Grenada	Extant	Native	-	Resident
Guadeloupe	Extant	Native	-	Resident
Guatemala	Extant	Native	-	Resident
Haiti	Extant	Native	-	Resident
Honduras	Extant	Native	-	Resident
Jamaica	Extant	Native	-	Resident
Martinique	Extant	Native	-	Resident
Mexico	Extant	Native	-	Resident
Montserrat	Extant	Native	-	Resident
Nicaragua	Extant	Native	-	Resident
Panama	Extant	Native	-	Resident
Puerto Rico	Extant	Native	-	Resident
Saint Kitts and Nevis	Extant	Native	-	Resident
Saint Lucia	Extant	Native	-	Resident
Saint Martin (French part)	Extant	Native	-	Resident
Saint Vincent and the Grenadines	Extant	Native	-	Resident
Sint Maarten (Dutch part)	Extant	Native	-	Resident
Trinidad and Tobago	Extant	Native	-	Resident

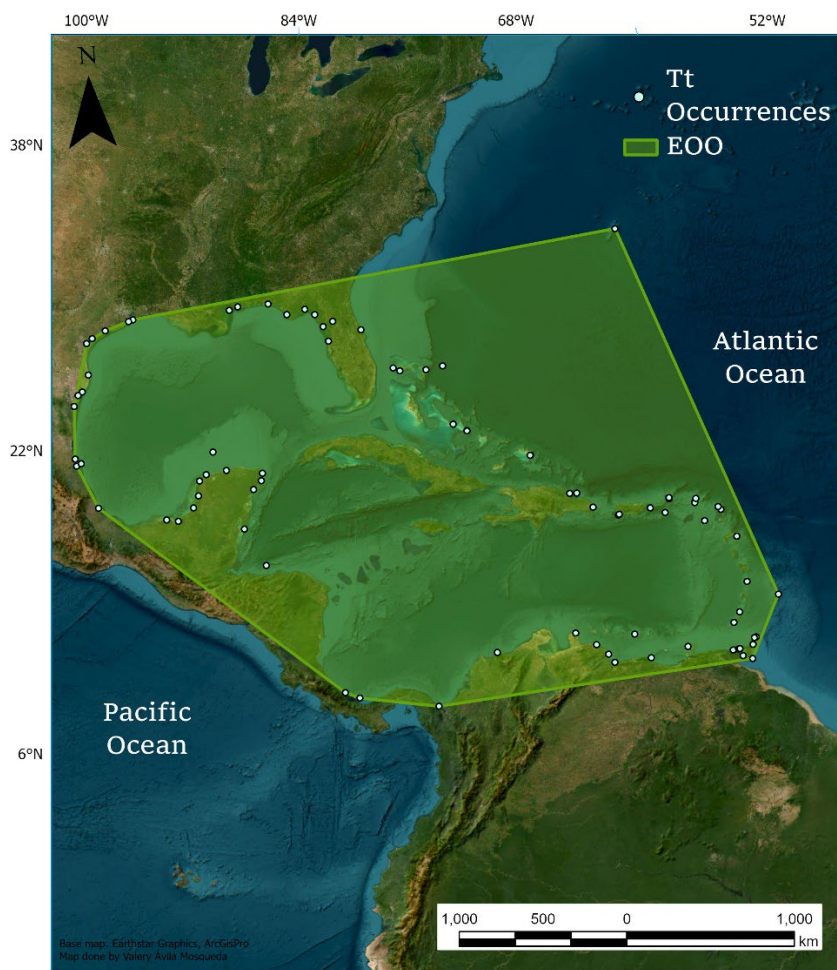
² This listing includes countries from this regional assessment and those reported for Bioregion 2 in the previous global assessment of *Thalassia testudinum* (Short et al. 2010).

Turks and Caicos Islands	Extant	Native -	Resident
United States of America	Extant	Native -	Resident
Venezuela, Bolivarian Republic of	Extant	Native -	Resident
Virgin Islands, British	Extant	Native -	Resident
Virgin Islands, U.S.	Extant	Native -	Resident

FAO Area Occurrence

Presence Origin Formerly Bred Seasonality			
31. Atlantic - western central	Extant	Native -	Resident

Regional Assessment Map ³



³ EOO was obtained using minimum bounding geometry/convex hull from ArcGIS Pro, giving the smallest polygon enclosing all points of occurrence.

Population

Thalassia testudinum forms extensive dense and stable seagrass meadows throughout its range. This is the most important and the largest seagrass habitat-forming species in the Greater Caribbean. Throughout the Greater Caribbean, in meadows dominated by *T. testudinum*, annual productivity of its leaves varies by an order of magnitude between 200 and 2000 g dry m⁻² y⁻¹. Large differences in biomass among meadows are registered; leaf biomass varies 1.5 -165 g dry m⁻², and total biomass (above and below ground tissues) varies between 108 and 1960 g dry m⁻² (Van Tussenbroek et al. 2014).

Since 2007, there have been increasing declines in meadow extension, or density of *T. testudinum* within multi-specific seagrass meadows, particularly in areas of nutrient enrichment and sedimentation. Other cases of increasing decline are linked to macroalgal blooms, excessive turtle grazing, competition with the invasive seagrass *Halophila stipulacea*, and synergic impacts of community shifts and usual natural disturbances (e.g., Van Tussenbroek et al. 2014). Although this species is still abundant throughout its range; the recent and continuing population decline, by loss of meadow extension or loss within meadows due to community shifts, combined with recurring disturbances, is a worrying trend. As an example of recurrence, *T. testudinum* populations suffered a large die-off of in Florida Bay from 1987-1990 (Durako & Hall 2000), but it was slowly recovering afterwards. However, in 2015, a second die-off episode occurred before the meadow had recovered (Hall et al. 2016). Also, the effects of die-offs are noticeable beyond the affected meadow, as primary die-off, followed by reduced water clarity and an increase in epiphytic growth, likely leads to secondary die-off among neighboring local seagrass (Nuttall et al. 2003).

Since the previous assessment in 2007, decreasing dominance of *T. testudinum* with increasing abundance of opportunistic or introduced seagrass and algal species, and/or decrease in meadow extensions have become more widespread throughout its whole distribution area (see Threats).

Population Information

Continuing decline in mature individuals? Qualifier Justification

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Continuing decline in number of subpopulations Qualifier Justification

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Habitats and Ecology

Thalassia testudinum is the most dominant and largest seagrass species in the Caribbean. This seagrass forms dense rhizome mats below the sediment, creating extensive meadows on shallow sand or mud substrates from the lower intertidal to a maximum 10-12 m depth. It has also been reported occasionally at ~ 20 m depth. Optimum temperatures for this species range between 20-30°C (Phillips 1960).

T. testudinum typically dominates seagrass vegetation in oligotrophic reef lagoons, where it often coexists with *Syringodium filiforme*, *Halodule wrightii* and calcareous rhizophytic green algae belonging to the order Caulerpaceae, amongst which *Halimeda* spp. are the most conspicuous members. This species is typically found in low density in oligotrophic areas and replaced by opportunistic and smaller species when there are continuous high nutrient inputs (Fourqurean & Rutten 2004).

This seagrass is an important food source for green sea turtles and manatees (which are both threatened species), as well as for a number of other fish and invertebrate species. It provides habitat to a wide variety of flora and fauna (Heck et al. 1979, Van Tussenbroek et al. 2006, Bologna et al. 2008).

Ecosystem services provided by *T. testudinum* include coastal protection (James et al. 2019;), carbon sequestration i.e. (Fourqurean et al. 2012; Armitage & Fourqurean 2016; Barry et al. 2018; López-Mendoza et al. 2020), supporting fisheries (May-Ku et al. 2014), nutrient recycling and retention (Delgado et al. 2017), supporting biodiversity (habitat

provision; Bologna et al. 2018, Montoya-Maya 2017; Samper-Villarreal et al. 2008, Otero Otero 2010; Bitter et al. 2009; Briones-Fourzán et al. 2020).

IUCN Habitats Classification Scheme

Habitat	Season	Suitability	Major Importance?
9.4. Marine Neritic -> Marine Neritic - Subtidal Sandy	-	Suitable	-
9.5. Marine Neritic -> Marine Neritic - Subtidal Sandy-Mud	-	Suitable	-
9.6. Marine Neritic -> Marine Neritic - Subtidal Muddy	-	Suitable	-
9.8.2. Marine Neritic -> Marine Neritic - Coral Reef -> Back Slope	-	Suitable	-
9.8.4. Marine Neritic -> Marine Neritic - Coral Reef -> Lagoon	-	Suitable	-
9.8.5. Marine Neritic -> Marine Neritic - Coral Reef -> Inter-Reef Soft Substrate	-	Suitable	-
9.9. Marine Neritic -> Marine Neritic - Seagrass (Submerged)	-	Suitable	-
9.10. Marine Neritic -> Marine Neritic - Estuaries	-	Suitable	-
12.2. Marine Intertidal -> Marine Intertidal - Sandy Shoreline and/or Beaches, Sand Bars, Spits, Etc	-	Suitable	-
12.4. Marine Intertidal -> Marine Intertidal - Mud Flats and Salt Flats	-	Suitable	-
12.6. Marine Intertidal -> Marine Intertidal - Tidepools	-	Suitable	-
12.7. Marine Intertidal -> Marine Intertidal - Mangrove Submerged Roots	-	Suitable	-

Life History

Generation Length	Justification	Data Quality
8	-	-

Thalassia testudinum populations can be maintained vegetative reproduction via (clonal) propagation by the below-ground rhizomes (Van Tussenbroek et al. 2006). Sexual reproduction contributes to the within-population genetic variation, and enabling long distance dispersal through floating fruits (van Dijk et al. 2009, 2018). Not all populations produce seeds, but some produce >500 seeds m⁻² annually (Van Katwijk et al. 2021).

T. testudinum is dioecious with male and female plants; pollination occurs through both water movement and small zoobenthic fauna (Van Tussenbroek et al. 2016). The seeds are viviparous and do not form seed banks (Van Tussenbroek et al. 2006). After major eradication, recolonization is dependent on import from seeds from other areas spread in floating fruits (Van Dijk et al. 2009), or from vegetative fragments (Van Tussenbroek et al. 2006). The generation length of this species has been estimated as eight years, although this may be much higher as the species can be very long-lived (several hundreds of years, Bricker et al. 2018; Van Dijk & Van Tussenbroek 2010). The minimal time of seedlings becoming reproductive is 4 years (Thorhaug 1979). Across its range, *T. testudinum* has very limited regional population structure, with two significant genetic partitions: (a) the Caribbean and (b) the Gulf of Mexico (Van Dijk et al. 2018).

Breeding Strategy

Does the species lay eggs?
NA

Does the species give birth to live young

NA

Does the species exhibit parthenogenesis

NA

Does the species have a free-living larval stage?
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NA

Does the species require water for breeding?

NA

Systems

System: Marine

Threats

Causes for population declines 2007-2020:

1. Ongoing eutrophication and sedimentation cause shifts in seagrass communities favoring other species over *Thalassia testudinum*.

The regional monitoring Program CARICOMP found increasing eutrophication and sedimentation at almost all 23 long-term monitoring sites (1993-2012), resulting in decrease of the relative abundance of *T. testudinum* with increasing abundance of faster growing seagrasses (*Syringodium filiforme*/*Halodule wrightii*) or macroalgae. Decreasing abundance of *T. testudinum* with increasing nutrient load before and during the assessment period has also been reported in Tampa Bay (Tampa Bay Estuary Program, 2001), Belize (Short et al. 2006), Florida Bay (Armitage et al. 2011), Curaçao (Govers et al. 2014), Cuba (Martinez-Daranas & Suarez 2018), and Bahamas (Stoner et al. 2014). In the Indian River Lagoon, seagrass communities have lost more than 50% of their pre-bloom areal extent in response to chronic, widespread phytoplankton blooms since 2011; *T. testudinum* populations have suffered serious declines throughout the system (Morris et al. 2021). Turtle grass habitat is lost in areas that were previously considered as near pristine in Belize (Gaston et al. 2009).

2. Recurring massive die-off in Florida Bay (Hall et al. 2016).

Causes of this mass mortality are thought to be hypersalinity, water column stratification and bottom-water anoxia (Johnson et al. 2018).

3. Algal blooms.

Sargassum Brown Tides caused by recent (since 2011) and massive bloom of holopelagic *Sargassum* species throughout the tropical Atlantic, caused mortality of *T. testudinum* in near coastal fringes of meadows (Van Tussenbroek et al. 2017; Bartlett & Elmer 2021), which are unlikely to recover due to the recurrent nature of the massive influx of *Sargassum* spp. (Wang et al. 2019). In Florida Bay, *T. testudinum* meadows were lost due to a macro-algal bloom of green macroalgae *Anadyomene* spp. (Santos et al. 2020). Macro-algal blooms are expected to occur more frequently with increasing coastal development (Lyons et al. 2014).

4. Overgrazing by sea turtles

Overgrazing by green turtles (*Chelonia mydas*) has caused an almost complete loss of *T. testudinum* (and other seagrasses) at all sites on the Bermuda Platform (Fourqurean et al. 2010, 2019). Excessive grazing has also affected *T. testudinum* elsewhere (Mexico-Molina Hernández-Molina & Van Tussenbroek 2014, US Virgin Islands - Williams 1988). Intensive grazing, similar to eutrophication, may also cause shifts in seagrass communities; favoring faster-growing species over the climax species *T. testudinum* (Martinez-López et al. 2019; Christianen et al. 2021)). Green turtle populations are expected to increase due to effective conservation measures (Heithaus et al. 2014; Christianen et al. 2021).

5. Invasive *Halophila stipulacea*

In disturbed areas the introduced seagrass *H. stipulacea* may outcompete native seagrasses including *T. testudinum* (Smulders et al. 2017). *H. stipulacea* is spreading fast throughout the Caribbean (Willette et al. 2014).

6. Ongoing localized pressures by urbanization and tourism

Pressure on the Caribbean coasts are increasing, and coastal seagrass meadows are amongst others threatened by tourism (e.g. Herrera-Silveira et al. 2010) and boat traffic (scarring; Furman et al. 2019). The slow growing *T. testudinum* needs a decade or decades to recover once lost (Furman et al. 2019, Van Tussenbroek, unpubl. data).

7. Oil spills

In Morrocoy, Venezuela, *T. testudinum* meadows have been impacted by recent oil spills (Beatriz Vera, unpublished)

8. Synergic influence of anthropogenic and natural disturbances

Undisturbed meadows dominated by the deeply rooted and robust *T. testudinum* are resistant against hurricanes (Cruz-Palacios & van Tussenbroek 2005). However, when shifts in seagrass communities occur, favoring faster-growing species, the meadows become more vulnerable to natural physical disturbances, resulting in collapse of local meadows (e.g. Barbados in Van Tussenbroek et al. 2014).

Conservation

The range of *Thalassia testudinum* falls in some Marine Protected Areas (MPAs). In the Caribbean, *T. testudinum* is included in the 24 fully managed marine protected areas. This species has been monitored by the CARICOMP network (Caribbean Coastal Marine Productivity network; Van Tussenbroek et al. 2014; Cortes et al. 2019), and is monitored at some places by SeagrassNet (<http://www.seagrassnet.org/>). This species is listed as Vulnerable (A2a) under the Bermuda Protected Species Act (Sarkis pers. comm. 2007). In Mexico, this species is protected under NOM-059 (Norma Oficial Mexicana; https://www.dof.gob.mx/nota_detalle_popup.php?codigo=5578808).

This is a major habitat-forming species in the Greater Caribbean (Van Tussenbroek et al. 2006) and should be monitored. If possible, active restoration efforts should be carried out where *T. testudinum* loss has occurred, when causing factors have been removed. Natural recovery rates are known to be very slow (e.g. Furman et al. 2019).

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Bibliography

- Armitage, A. R., Frankovich, T. A., & Fourqurean, J. W. (2011). Long-term effects of adding nutrients to an oligotrophic coastal environment. *Ecosystems*, 14(3), 430-444.
- Armitage, A. R., & Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *ifldr Import 2019-10-08 Batch 5*.
- Barry, S. C., Bianchi, T. S., Shields, M. R., Hutchings, J. A., Jacoby, C. A., & Frazer, T. K. (2018). Characterizing blue carbon stocks in *Thalassia testudinum* meadows subjected to different phosphorus supplies: A lignin biomarker approach. *Limnology and Oceanography*, 63(6), 2630-2646.
- Bartlett, D., Elmer, F. (2021). The impact of Sargassum inundations on the Turks and Caicos Islands. *Phycology*, 1(2), 83-104.
- Bitter, R., Didonna, G., & Viéitez, J. (2009). Caracterización de la comunidad de moluscos asociada a *Thalassia testudinum* en localidades del Parque Nacional Morrocoy, Venezuela. *Ciencia*, 17(2).
- Bologna, P. A., Papagian, R., Regetz, S., & Dale, C. (2008). Assessment of turtle grass (*Thalassia testudinum* ex Banks König) community structure in a UNESCO Biosphere Reserve. *Journal of experimental marine biology and ecology*, 365(2), 148-155.
- Bricker, E., Calladine, A., Virnstein, R., & Waycott, M. (2018). Mega clonality in an aquatic plant—a potential survival strategy in a changing environment. *Frontiers in plant science*, 9, 435.
- Briones-Fourzán, P., Monroy-Velázquez, L. V., Estrada-Olivo, J., & Lozano-Álvarez, E. (2020). Diversity of Seagrass-Associated Decapod Crustaceans in a Tropical Reef Lagoon Prior to Large Environmental Changes: A Baseline Study. *Diversity*, 12(5), 205.
- Christianen, M. J., van Katwijk, M. M., van Tussenbroek, B. I., Pagès, J. F., Ballorain, K., Kelkar, N., R. Arhtur & Alcoverro, T. (2021). A dynamic view of seagrass meadows in the wake of successful green turtle conservation. *Nature Ecology & Evolution*, 5: 553-555.

- Cortés, J., Oxenford, H. A., van Tussenbroek, B. I., Jordán-Dahlgren, E., Cróquer, A., Bastidas, C., & Ogden, J. C. (2019). The CARICOMP network of Caribbean Marine Laboratories (1985–2007): history, key findings, and lessons learned. *Frontiers in Marine Science*, 5, 519.
- Cruz-Palacios, V., & Van Tussenbroek, B. I. (2005). Simulation of hurricane-like disturbances on a Caribbean seagrass bed. *Journal of Experimental Marine Biology and Ecology*, 324(1), 44-60.
- Delgado, M., Cintra-Buenrostro, C. E., & Fierro-Cabo, A. (2017). Decomposition and nitrogen dynamics of turtle grass (*Thalassia testudinum*) in a subtropical estuarine system. *Wetlands Ecology and Management*, 25(6), 667-681.
- Duarte, C. M. (1991). Seagrass depth limits. *Aquatic botany*, 40(4), 363-377.
- Durako, M.J. & Hall, M.O. (2000). After the die-off: Seagrass dynamics in a perturbed subtropical lagoon. *Biologia Marina Mediterranea* 7(2): 365-368.
- Fourqurean, J.W. & Rutten, L.M. (2004). The impact of Hurricane Georges on soft-bottom, back reef communities: site- and species-specific effects in south Florida seagrass beds. *Bulletin of Marine Science* 75(2): 237-257.
- Fourqurean, J. W., Manuel, S., Coates, K. A., Kenworthy, W. J., & Smith, S. R. (2010). Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series*, 419, 223-232.
- Fourqurean, J. W., Manuel, S. A., Coates, K. A., Massey, S. C., & Kenworthy, W. J. (2019). Decadal Monitoring in Bermuda Shows a Widespread Loss of Seagrasses Attributable to Overgrazing by the Green Sea Turtle *Chelonia mydas*. *Estuaries and Coasts*, 42(6), 1524-1540.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., ... & Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature geoscience*, 5(7), 505-509.
- Furman, B. T., Merello, M., Shea, C. P., Kenworthy, W. J., & Hall, M. O. (2019). Monitoring of physically restored seagrass meadows reveals a slow rate of recovery for *Thalassia testudinum*. *Restoration Ecology*, 27(2), 421-430.
- Gaston, G. R., Easson C., Easson G., Janaskie J. & Ballas M. (2009). Seagrass loss in Belize: Studies of turtlegrass (*Thalassia testudinum*) habitat using remote sensing and ground-truth data. *Gulf and Caribbean Research* 21 (1): 23-30.
- Govers, L. L., Lamers, L. P., Bouma, T. J., de Brouwer, J. H., & van Katwijk, M. M. (2014). Eutrophication threatens Caribbean seagrasses—An example from Curaçao and Bonaire. *Marine pollution bulletin*, 89(1-2), 481-486.
- Hall, M. O., Furman, B. T., Merello, M., & Durako, M. J. (2016). Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: initial observations. *Marine ecology progress series*, 560, 243-249.
- Heck Jr, K. L. (1979). Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. *Journal of biogeography*, 183-200.
- Heithaus, M. R., Alcoverro, T., Arthur, R., Burkholder, D. A., Coates, K. A., Christianen, M. J., ... & Fourqurean, J. W. (2014). Seagrasses in the age of sea turtle conservation and shark overfishing. *Frontiers in Marine Science*, 1, 28.
- Herrera-Silveira, J. A., Cebrian, J., Hauxwell, J., Ramirez-Ramirez, J., & Ralph, P. (2010). Evidence of negative impacts of ecological tourism on turtlegrass (*Thalassia testudinum*) beds in a marine protected area of the Mexican Caribbean. *Aquatic Ecology*, 44(1), 23-31.
- James, R. K., Silva, R., van Tussenbroek, B. I., Escudero-Castillo, M., Mariño-Tapia, I., Dijkstra, H. A., ... & Van der Boog, C. G. (2019). Maintaining tropical beaches with seagrass and algae: a promising alternative to engineering solutions. *BioScience*, 69(2), 136-142.
- Johnson, C. R., Koch, M. S., Pedersen, O., & Madden, C. J. (2018). Hypersalinity as a trigger of seagrass (*Thalassia testudinum*) die-off events in Florida Bay: evidence based on shoot meristem O₂ and H₂S dynamics. *Journal of Experimental Marine Biology and Ecology*, 504, 47-52.
- Juman, R., & Alexander, K. J. (2006). An Inventory of Seagrass Communities Around Trinidad and Tobago. Institute of Marine Affairs, Chaguaramas.
- López-Mendoza, P. G., Ruiz-Fernández, A. C., Sanchez-Cabeza, J. A., Van Tussenbroek, B. I., Cuellar-Martinez, T., & Pérez-Bernal, L. H. (2020). Temporal trends of organic carbon accumulation in seagrass meadows from the northern Mexican Caribbean. *Catena*, 194, 104645.
- Lyons, Devin A., Christos Arvanitidis, Andrew J. Blight, Eva Chatzinikolaou, Tamar Guy-Haim, Jonne Kotta, Helen Orav-Kotta et al. (2014). Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Global change biology* 20(9): 2712-2724.
- Hernández-Molina, A. L. & Van Tussenbroek, B. I. (2014). Patch dynamics and species shifts in seagrass communities under moderate and high grazing pressure by green sea turtles. *Marine ecology progress series*, 517, 143-157.
- Martínez-Daranas, B., & Suárez, A.M. (2018). An overview of Cuban seagrasses. *Bulletin of marine science*, 94(2), 269-282.
- Martinez López, I. G., van Den Akker, M., Walk, L., van Katwijk, M. M., van Der Heide, T., & van Tussenbroek, B. I. (2019). Nutrient availability induces community shifts in seagrass meadows grazed by turtles. *PeerJ*, 7, e7570.
- Montoya Maya, P. (2017). Evaluación de la macrofauna epibentónica asociada a praderas de *Thalassia testudinum* (Banks ex König) en el Caribe Colombiano (Bachelor's thesis, Universidad de Bogotá Jorge Tadeo Lozano).

- Morris, L. J., Hall, L. M., Miller, J. D., Lasi, M. A., Chamberlain, R. H., Virnstein, R. W., & Jacoby, C. A. (2021). Diversity and distribution of seagrasses as related to salinity, temperature, and availability of light in the Indian River Lagoon, Florida. *Florida Scientist*, 84(2/3), 119-137.
- Otero Otero, A. (2010). Macroinvertebrados asociados a pastos marinos (*Thalassia testudinum*) en el Golfo de Morrosquillo (Zona de Berrugas) Departamento de Sucre.
- Samper-Villarreal, J., Bernecker, A., & Wehrtmann, I. S. (2008). Inventory of macroalgal epiphytes on the seagrass *Thalassia testudinum* (Hydrocharitaceae) in Parque Nacional Cahuita, Caribbean coast of Costa Rica. *Revista de biología tropical*, 163-174.
- Samper-Villarreal, J., Bernecker, A., & Wehrtmann, I. S. (2008). Inventory of macroalgal epiphytes on the seagrass *Thalassia testudinum* (Hydrocharitaceae) in Parque Nacional Cahuita, Caribbean coast of Costa Rica. *Revista de biología tropical*, 163-174.
- Santos, R. O., Varona, G., Avila, C. L., Lirman, D., & Collado-Vides, L. (2020). Implications of macroalgae blooms to the spatial structure of seagrass seascapes: The case of the *Anadyomene* spp. (Chlorophyta) bloom in Biscayne Bay, Florida. *Marine pollution bulletin*, 150, 110742.
- Short, F.T., E. Koch, J.C. Creed, K.M. Magalhaes, E. Fernandez, J.L. Gaeckle. 2006. SeagrassNet monitoring across the Americas: case studies of seagrass decline. *Marine Ecology* 27, 277-289.
- Short, F.T., Carruthers, T.J.R., van Tussenbroek, B. & Zieman, J. 2010. *Thalassia testudinum*. The IUCN Red List of Threatened Species 2010: e.T173346A6995927. <https://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T173346A6995927.en>. Accessed on 14 May 2025.
- Smulders, F. O., Vonk, J. A., Engel, M. S., & Christianen, M. J. (2017). Expansion and fragment settlement of the non-native seagrass *Halophila stipulacea* in a Caribbean bay. *Marine biology research*, 13(9), 967-974.
- Stoner, E. W., Yeager, L. A., Sweatman, J. L., Sebilian, S. S., & Layman, C. A. (2014). Modification of a seagrass community by benthic jellyfish blooms and nutrient enrichment. *Journal of experimental marine biology and ecology*, 461, 185-192.
- Tampa Bay Estuary Program. (2001). Tracking Progress Toward Its Nitrogen Management Goals: Fifth-Year Assessment of Bay Water Quality Indicators and Models. Prepared by Janicki Environmental, Inc. for the Tampa Bay Estuary Program, St. Petersburg, FL
- Thorhaug, A. (1979). The flowering and fruiting of restored *Thalassia* beds: a preliminary note. *Aquatic botany*, 6, 189-192.
- Van Dijk, J. K., van Tussenbroek, B. I., Jiménez-Durán, K., Márquez-Guzmán, G. J., & Ouborg, J. (2009). High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. *Marine ecology progress series*, 390, 67-77.
- Van Dijk, J. K., & van Tussenbroek, B. I. (2010). Clonal diversity and structure related to habitat of the marine angiosperm *Thalassia testudinum* along the Atlantic coast of Mexico. *Aquatic botany*, 92(1), 63-69.
- Van Dijk, K. J., Bricker, E., van Tussenbroek, B.I., & Waycott, M. (2018). Range-wide population genetic structure of the Caribbean marine angiosperm *Thalassia testudinum*. *Ecology and evolution*, 8(18), 9478-9490.
- Van Katwijk, M. M., van Tussenbroek, B. I., Hanssen, S. V., Hendriks, A. J., & Hanssen, L. (2021). Rewilding the sea with domesticated seagrass. *BioScience*, 71(11), 1171-1178.
- Van Tussenbroek, B. I. V., Vonk, J. A., Stapel, J., ... & Zieman, J. C. (2006). The biology of *Thalassia*: paradigms and recent advances in research, In (eds) Larkum, A. W., Orth, R. J., Duarte, C. M., Seagrasses: Biology, Ecology and Conservation, (pp. 409-439). Springer Netherlands.
- Van Tussenbroek, B. I., Cortés, J., Collin, R., Fonseca, A. C., Gayle, P. M., Guzmán, H. M., ... & Rodríguez-Ramírez, A. (2014). Caribbean-wide, long-term study of seagrass beds reveals local variations, shifts in community structure and occasional collapse. *PloS one*, 9(3), e90600.
- Van Tussenbroek, B.I., Villamil, N., Márquez-Guzmán, J., Wong, R., Monroy-Velázquez, L. V., & Solis-Weiss, V. (2016). Experimental evidence of pollination in marine flowers by invertebrate fauna. *Nature communications*, 7(1), 12980.
- Van Tussenbroek, B.I., Arana, H.A.H., Rodríguez-Martínez, R.E., Espinoza-Avalos, J., Canizales-Flores, H. M., González-Godoy, C. E., ... & Collado-Vides, L. (2017). Severe impacts of brown tides caused by *Sargassum* spp. on near-shore Caribbean seagrass communities. *Marine pollution bulletin*, 122(1-2), 272-281.
- Wang, M., Hu, C., Barnes, B. B., Mitchum, G., Lapointe, B., & Montoya, J. P. (2019). The great Atlantic sargassum belt. *Science*, 365(6448), 83-87.
- Williams, S. L. (1988). *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Marine biology*, 98(3), 447-455.