

Review

Seagrasses in the Eastern Tropical Pacific: species, distribution ecology, blue carbon, and threats

Jimena Samper-Villarreal¹ 

¹Centro de Investigación en Ciencias del Mar y Limnología (CIMAR)
Universidad de Costa Rica, San José, Costa Rica
Corresponding author: Jimena Samper-Villarreal (jimena.sampervillarreal@ucr.ac.cr)

ABSTRACT. Eastern Tropical Pacific (ETP) seagrasses are composed of three genera and four species: *Halophila baillonii*, *Halodule beaudettei*, *Halodule wrightii*, and *Ruppia maritima*. These are colonizing seagrass species and meadows in the ETP can be ephemeral. Current seagrass distribution in this region remains unknown, with verified extant presence at a limited number of locations and mapping heavily reliant on historical reports. Suitable environmental conditions for seagrasses in the ETP consist of sheltered bays <10 m depth with fine sediment, 19-35 salinity, 26-32°C temperature, and water transparency of up to 10 m Secchi depth. In this region, seagrass organic carbon (OC) biomass pools (<0.2 Mg ha⁻¹) have been reported from three locations, while sediment bulk density (<1.4 g mL⁻¹) and OC (<24 Mg ha⁻¹) have been reported from eight locations, all found on the Pacific coast of Costa Rica. Recent blue carbon reports from the ETP have not been included in global assessments to date. OC sequestration and sediment accumulation rates are currently unknown. Seagrasses provide key ecosystem services yet they are also threatened by anthropogenic and natural stressors. Seagrasses have already disappeared from two locations within the ETP, with restoration efforts currently underway on the northern Pacific coast of Costa Rica. This overview of our current understanding of seagrasses in the ETP and their services highlights the need for further research in this understudied region.

Keywords: seagrass meadows; coastal habitats; organic carbon; carbon sequestration; Costa Rica; Central America

INTRODUCTION

Seagrass is a term used for vascular flowering plants (Monocotyledoneae, Alismatales) that can live and reproduce completely submerged in salty water and form a highly productive coastal habitat known as seagrass meadows. Seagrasses are an ecological group, with 72 species of aquatic plants currently considered to be seagrasses (Short et al. 2011). Unfortunately, seagrass meadows are highly threatened coastal habitats and vast areas of them have been degraded or lost (Orth et al. 2006, Waycott et al. 2009). In the IUCN Red List global extinction risk assessments, 24% of all seagrass species are considered to be Threatened or

Near Threatened. Meanwhile, the extinction risk level of 12% of seagrass species remains unknown as they are considered Data Deficient (Short et al. 2011). To support seagrass conservation, management, and ecological restoration initiatives, current gaps in our understanding of seagrass meadows need to be addressed.

Seagrass meadows provide many ecosystem services which can vary within and among meadows. Seagrasses support complex food webs including commercially and ecologically important species; they function as a nursery habitat, provide coastline protection, and serve as carbon sinks thereby supporting global initiatives for climate change mitigation

(Duarte et al. 2013, Nordlund et al. 2018). Organic carbon (OC) stored in seagrass meadows and other marine vegetated ecosystems, such as mangroves and salt marshes, is commonly referred to as "blue carbon" (McLeod et al. 2011). Globally, while seagrass meadows often store the lowest amounts of OC per hectare of these three habitats, they are the only ecosystem abundant in both temperate and tropical climates and can, therefore, sequester larger amounts of OC overall (McLeod et al. 2011). Within seagrass meadows, OC is stored mainly in the associated sediment and represents an average of 2.5% of the sediment at a global scale. Seagrass biomass protects sediment OC pools and promotes OC sequestration while also storing around 2.5 Mg OC ha⁻¹ in living tissues (Fourqurean et al. 2012). Both biotic and abiotic factors can lead to variability in OC storage in seagrass meadows (Mazarrasa et al. 2018). However, blue carbon studies have mainly focused on OC sequestration in meadows of large species in temperate regions, such as *Posidonia oceanica* (Fourqurean et al. 2012). Thus, increased research on OC storage dynamics in meadows composed of smaller seagrass species and within understudied regions is currently needed.

While we are clear on their carbon sink capacity, many uncertainties remain regarding blue carbon in seagrass meadows. For instance, despite many recent technological advances, there are continued challenges in mapping seagrasses, particularly those found in deeper or murkier waters and those composed of smaller species (Roelfsema et al. 2014, Hossain et al. 2015). Furthermore, while there has been great advancement in seagrass blue carbon in some regions, such as Australia (Serrano et al. 2019), there are many regions where we know very little about carbon stocks and burial rates (Fourqurean et al. 2012). These understudied regions are found mainly in the tropics and areas with limited research funding and capability. Moreover, seagrasses are highly threatened ecosystems with frequent loss or degradation of seagrass meadows in many regions (Orth et al. 2006, Waycott et al. 2009). It is not possible to effectively manage, conserve, or restore these habitats if there is a void in basic information such as their distribution and ecological dynamics.

The Eastern Tropical Pacific (ETP) is an area where we know very little not only about seagrass carbon stocks and burial rates, but of seagrasses in general. Given the need for further seagrass research in this understudied region, the aim of this work is to provide an overview of the current understanding of seagrasses

in the ETP, highlight key gaps, and propose potential pathways to fill them. Included studies were compiled by searching for publications in English and Spanish in peer-reviewed journals, reports, theses, and other grey literature. These publications were obtained by searches using the term "seagrass" in English and Spanish and the seagrass species known to occur within the ETP in Google Scholar, university repositories, and provided by colleagues. Literature was compiled, summarized, and is critically reviewed here.

Seagrasses in the Eastern Tropical Pacific (ETP)

The ETP is a marine region that includes the warm waters off the western coast of Central America, located within the Equatorial Pacific (Fig. 1). It is limited by the colder waters found in the North and South Pacific subtropical gyres. As such, the ETP is limited by Baja California in the north, with the influence of the California Current southwards. In the south, the ETP is limited by Peru, with the Humboldt Current bringing colder waters northwards (Fiedler & Talley 2006, Fiedler et al. 2013).

Species and life strategies

Seagrasses in the ETP are part of the Tropical Atlantic (TA) seagrass bioregion (Short et al. 2007), which holds 42% of the world's seagrass distribution (McKenzie et al. 2020). The TA seagrass bioregion has high species diversity, with 10 species reported growing in various coastal environments, including coastal and reef lagoons, near mangroves, and shallow banks (Short et al. 2007). Only four of the 10 TA seagrass species are found in the ETP: *Halophila baillonii* (Hydrocharitaceae), *Halodule beaudettei*, *Halodule wrightii* (Cymodoceaceae), and *Ruppia maritima* (Ruppiales) (Phillips & Meñez 1988, Green & Short 2003, Van Tussenbroek et al. 2010). As such, with only four species reported here, the ETP is a region with very low seagrass species diversity. In contrast, the highest seagrass species diversity is found in the Indo-Pacific, with up to 20 seagrass species (Short et al. 2011). Some of the other TA species would not be expected to occur in the ETP as they are exclusively found in the Caribbean, Atlantic, or African coastlines. *Thalassia testudinum*, for instance, is a TA species found exclusively in the Caribbean that has been incorrectly reported to occur historically in the ETP (Phillips & Meñez 1988, Green & Short 2003, Van Tussenbroek et al. 2010). This erroneous report is believed to be an incorrect interpretation of Den Hartog's 1970 report, stating it as "an unconfirmed record of *T. testudinum* in the Gulf of Panama".

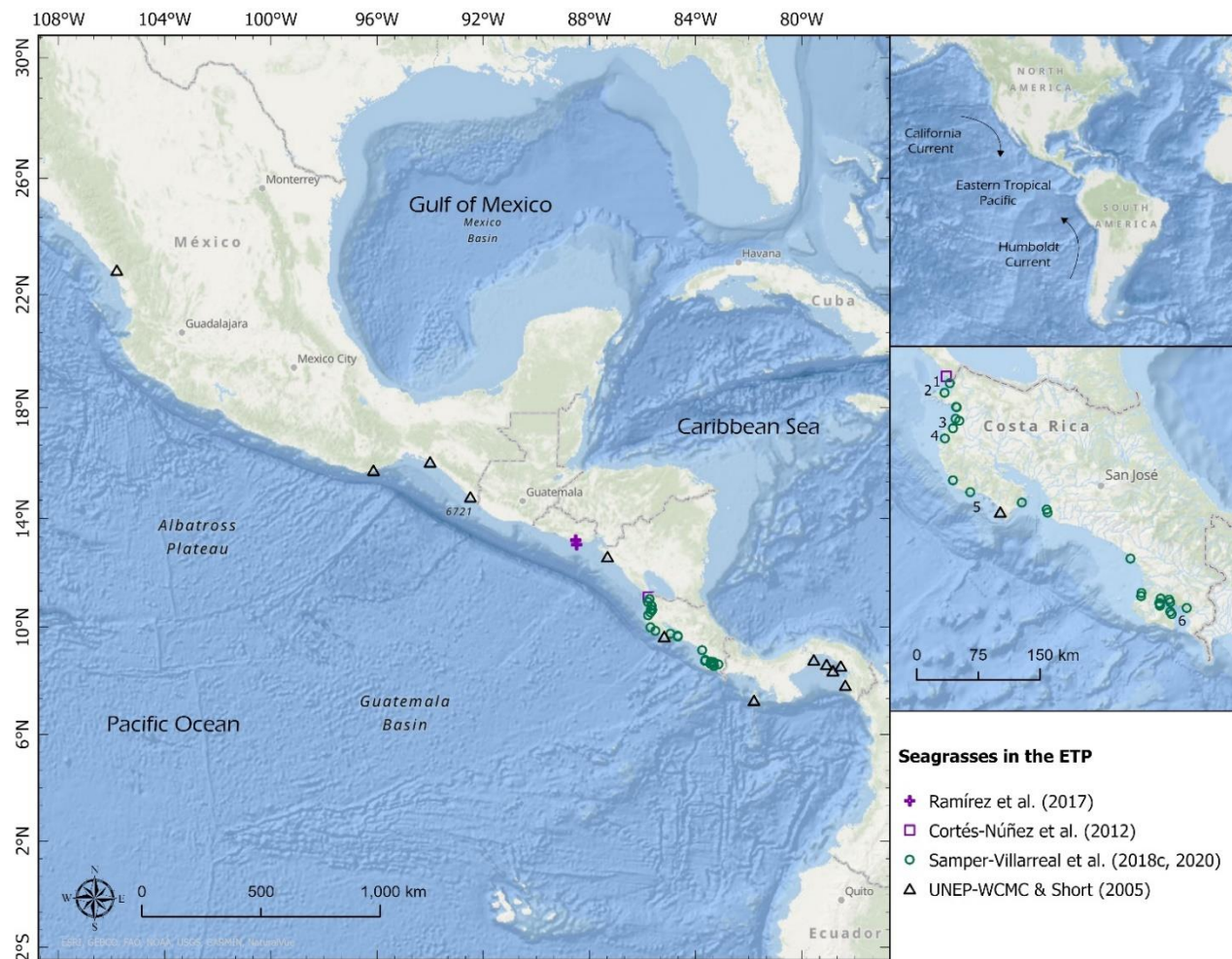


Figure 1. Seagrasses in the Eastern Tropical Pacific (ETP) based on historical records (UNEP-WCMC & Short 2005) and more recent reports from El Salvador (Ramírez et al. 2017), Nicaragua (Cortés-Núñez et al. 2012), and Costa Rica (Samper-Villarreal et al. 2018c, 2020). Top right panel showcases where the ETP is found within the globe, the left panel where seagrasses have been reported in the ETP, and the bottom right panel where the Pacific coast of Costa Rica is enlarged given the density of points. Numbers in the bottom right panel refer to specific locations within Costa Rica that are mentioned in the text: 1: El Jobo, 2: Matapalito, 3: Bahía Culebra, 4: Potrero, 5: Sámara, and 6: Golfo Dulce.

Previous nomenclature and current taxonomic challenges also need to be considered when defining the number of species found in the ETP. For instance, the clover grass, *Halophila baillonii*, has been previously misnamed as *Halophila baillonis* (Creed & Samper-Villarreal 2019). Meanwhile, *Halophila decipiens* has been wrongly reported to occur historically in the ETP (Phillips & Meñez 1988), which is considered an error from the misidentification of *H. baillonii* (Creed & Samper-Villarreal 2019). Recently, a phylogenomic study has reported that *H. baillonii* in fact originated in the Caribbean and may have passed through the Panama Canal to colonize the ETP, making it the only seagrass species to be considered non-native

in this region (Van Dijk et al. 2023). Furthermore, there is currently marked uncertainty among seagrass taxonomists worldwide regarding various species of *Halodule*. This taxonomic uncertainty is because identifying the different *Halodule* species is based mainly on leaf tip morphology (Den Hartog 1964, Kuo & Den Hartog 2001), which can vary greatly even within the same plant (Wheeler et al. 2020). At a global level, there are molecular taxonomy studies currently underway to clarify the taxonomic standing of many *Halodule* species.

Ruppia is an aquatic plant that can be found in a wide range of salinities, from freshwater lakes at high elevations to very low and very high salinity concen-

trations (Kantrud 1991, Den Hartog et al. 2016). It can thrive alongside brackish and freshwater species but is also often found growing intermixed with seagrass species (Kantrud 1991, Green & Short 2003). This has led some experts to consider excluding *Ruppia* from the list of seagrasses and refer to it as a freshwater species with high salinity tolerance (Kantrud 1991). The most common species is *R. maritima*, which has a wide global distribution and is included as one of the seagrass species in the world (Green & Short 2003, Short et al. 2011). As such, *R. maritima* has been included as a seagrass species for the ETP in this review. However, *Ruppia* seagrasses found in the ETP need to be analyzed using molecular tools to verify their taxonomy given the current uncertainty for some *Ruppia* species at a global scale and a new species recently reported from Mexico (*Ruppia mexicana*) (Den Hartog et al. 2016).

Furthermore, all three seagrass genera found in the ETP (*Halodule*, *Halophila*, and *Ruppia*) are considered to be colonizing seagrasses (Kilminster et al. 2015, O'Brien et al. 2018). This categorization is based on their overall life strategy, which includes the fact that they are fast growing with a high shoot turnover rate, the short time needed for their first flowering event to occur, and the fact that they have dormant seeds (Kilminster et al. 2015). Higher seed dormancy allows these seagrasses to form a seed bank in the sediment, which can germinate when conditions are viable following a perturbation or seagrass loss. Compared to larger and slower-growing species, these colonizing seagrasses generally have lower resistance thresholds to perturbations and greater recovery capacity (O'Brien et al. 2018). Therefore, seagrasses in the ETP are formed by a very limited number of small species, and the meadows are dynamic and ephemeral compared to more stable meadows dominated by larger species in other regions.

Distribution

Historically, seagrasses within the ETP were reported to occur only at sporadic locations (Fig. 1). In the world atlas of seagrasses (Green & Short 2003), ETP seagrasses encompassed only a limited number of locations with small areas (Green & Short 2003, UNEP-WCMC & Short 2005). These historical reports of seagrass distribution have been replicated over time without more recent field verification (Den Hartog 1964, 1970, Phillips & Meñez 1988, Green & Short 2003, Van Tussenbroek et al. 2010). A lack of *in situ* verification of seagrass presence may lead to inaccuracies in seagrass distribution within the ETP.

For example, in Costa Rica, the only historical report of seagrasses included in the atlas (Green & Short 2003, UNEP-WCMC & Short 2005) (Fig. 1) is considered incorrect. This report was placed indiscriminately on the Pacific coast of Costa Rica based on a historical report (Phillips & Meñez 1988) (Fred Short, *pers. comm.*). However, the hydrodynamic conditions overall in that area make it an unlikely location for seagrass presence. This highlights the need for *in situ* verification of whether seagrasses are currently present at these historical sites in the ETP to clarify the extant distribution of seagrasses in the region.

Recently, seagrasses have been reported as extant at multiple locations in the ETP, including El Salvador (MARN 2010, Ramírez et al. 2017), Nicaragua (Cortés-Núñez et al. 2012), and Costa Rica (Samper-Villarreal et al. 2018c, 2020) (Figs. 1-2). On the Pacific coast of El Salvador, a strip of seagrasses of ~4 km in length and a total area of ~27 km² was reported within a bay (MARN 2010, Ramírez et al. 2017). In Nicaragua, seagrasses were reported from one location yet the total seagrass area is currently unknown (Cortés-Núñez et al. 2012). On the Pacific coast of Costa Rica, seagrasses were reported from 21 locations, with an estimated total extent of ~100 ha (Samper-Villarreal et al. 2018c), and a limited number of locations subsequently added (Samper-Villarreal & Cortés 2020, Samper-Villarreal et al. 2020). The largest meadow in the ETP was reported to occur in Golfo Dulce, on the southern Pacific coast of Costa Rica (Fig. 1), with a reported area of up to ~90 ha (Samper-Villarreal et al. 2018c). However, it is now clear that the total area of the seagrasses on the Pacific coast of Costa Rica can vary seasonally (Barquero-Chanto 2018, Samper-Villarreal et al. 2020). Furthermore, the higher number of seagrass locations recently reported in Costa Rica is most likely a reflection of increased seagrass research efforts in this country and not a reflection of higher seagrass abundance. Therefore, while there has been an increase in recent reports of seagrasses within the ETP, the current known seagrass distribution still only includes a limited number of fragmented locations (Fig. 1), and the current area of seagrasses in the ETP is unknown.

Mapping methodologies used to delineate the seagrass distribution in the ETP have been mainly based on direct observation in the field. Aerial photography has proven useful for locating dense meadows in clear water and providing preliminary maps of seagrass distribution on the Pacific coast of Costa Rica (Cortés 2001). Key limitations to mapping seagrasses in the ETP include the small size of the

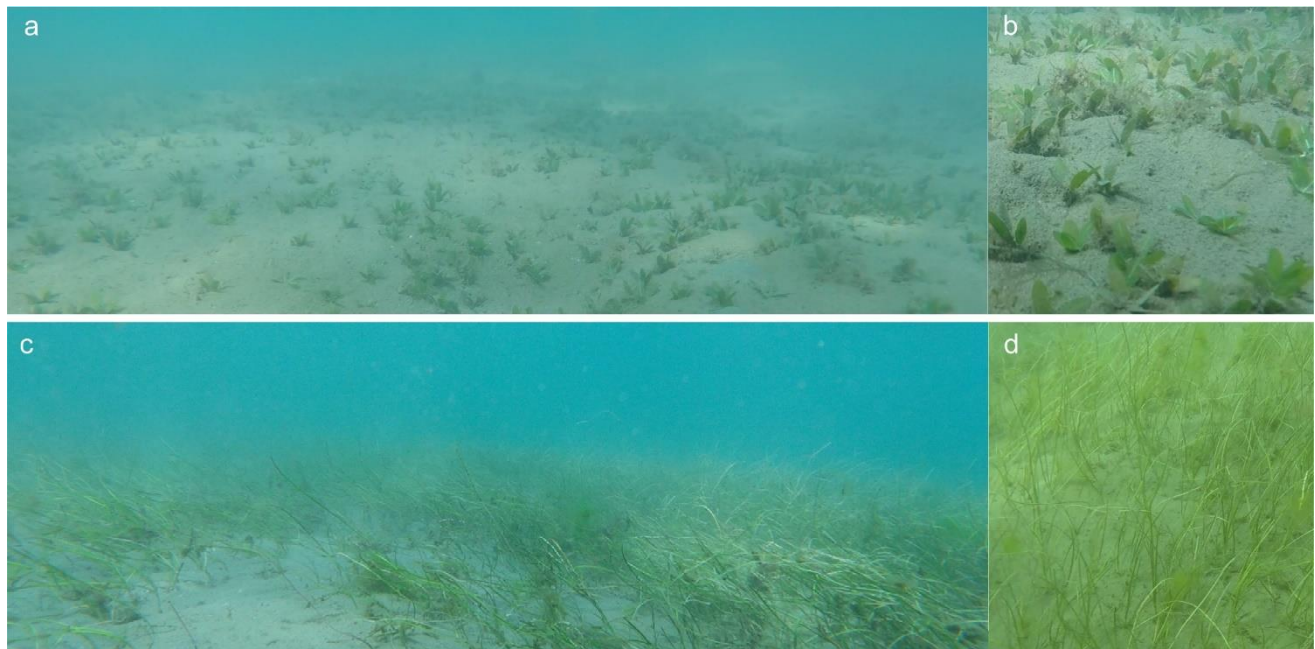


Figure 2. Field photos of seagrass meadows in the Eastern Tropical Pacific. a) *Halophila baillonii* meadow, b) a close-up of this species, c) *Halodule beaudettei* meadow, and d) a close-up of this species.

species present, low seagrass cover at many sites, temporal variability, water turbidity, and depth. Using remote sensing approaches to map seagrasses in more turbid waters, smaller species, or deeper areas is challenging (Roelfsema et al. 2014), and can potentially lead to an underestimation of the total seagrass area. As noted in the Southwestern Atlantic, mapping seagrasses of small leaves, such as *Halophila* can be challenging in turbid waters and clear water at greater depths (Hatje et al. 2023). Given these limitations, underwater field assessments by snorkel and SCUBA are considered the most effective way to assess seagrass presence in this region, yet they are costly and time-consuming. Direct underwater photographs and video or using autonomous underwater vehicles (AUVs) are considered a viable tool in the field for seagrass mapping efforts if the water is clear (Roelfsema et al. 2014, Veettil et al. 2020). Aerial drones are likely a viable form of seagrass mapping in areas of greater water transparency and seagrass density in this region. Georeferenced photo transects from the field could also be linked to remote sensing methods of seagrass mapping in clear waters and allow estimation of parameters such as species composition and biomass (Roelfsema et al. 2014). Mapping efforts in the ETP need to be strengthened and existing or novel mapping approaches that use less time and resources and allow analysis of larger areas should be tested in the region.

Understanding the type of environment in which ETP seagrass species are commonly found in other regions can provide insight into their potential spatial distribution within the ETP. *H. baillonii* has a very limited global distribution, with this species found only in the Caribbean, Atlantic, and the ETP (Phillips & Meñez 1988, Green & Short 2003, Short et al. 2010a, Van Dijk et al. 2023). This species is found in mud to fine sand substrates, mostly at 1-3 m but up to 15 m depths (Short et al. 2010a). *H. wrightii* is an ephemeral species that is abundant in many locations globally (Short et al. 2010b). This species is found in shallow areas with sand and mud substrate close to the coastline and is very tolerant to variations in salinity, temperature, turbidity, and nutrient loading (Short et al. 2010b).

Meanwhile, *H. beaudettei* is currently reported to have a limited global distribution (Green & Short 2003). Globally, these three seagrass species (*H. beaudettei*, *H. wrightii*, and *H. baillonii*) are limited to tropical conditions, while *R. maritima* can be found in both tropical and temperate locations. In coastal areas, *R. maritima* is found mostly in shallow and clear waters, with substrates composed of silt, clay, mud, or sand, and at a wide range of salinities (Kantrud 1991). This species has a root system that is shallow and weak and therefore usually found in still or calm conditions

such as lagoons or bays and is affected by marked fluctuations in circulation or water level (Kantrud 1991). Overall, these species grow in shallow areas of muddy to sandy substrates in calm conditions. Within the ETP, a useful approach to maximize mapping resources and efforts would be mathematical spatial modeling of suitable seagrass habitat (Saunders et al. 2013), considering depth, light availability, geomorphology, and hydrology for seagrasses in this region.

Environmental conditions for seagrass presence in the ETP

Our current knowledge of where seagrasses are found in the ETP region is limited. However, recent work provides key information towards understanding suitable environmental conditions for them to thrive within the ETP. On the Pacific coast of Costa Rica, seagrasses are usually found within calmer and more sheltered bays, as opposed to high-energy exposed areas. This is reflected in the sediment grain size at these locations, with sediment composed mostly of fine and very fine sand (Table 1). In El Salvador, seagrasses were found in a mangrove estuary complex with sediment composed of fine sand and mud (Ramírez et al. 2017). Therefore, seagrass locations within the ETP will likely include more sheltered and calmer areas dominated by fine sandy/muddy sediment.

Seagrasses need adequate light conditions for net photosynthetic productivity, with light availability linked to water depth and transparency. Seagrasses have been found at depths of <10 m in the Pacific coast of Costa Rica (Table 1) and at 5 m depth in Nicaragua (Cortés-Núñez et al. 2012). In Costa Rica, seagrasses are usually found submerged at low tide and would therefore be considered subtidal, only exposed at extreme low tide events for short periods. Seagrasses on this coast have been reported at varying water transparency conditions, with Secchi depths ranging from 0.2 to 10 m (Table 1). In El Salvador, water transparency has been reported to be between 1-2 m (Ramírez et al. 2017). In Costa Rica, seagrasses have been found at shallower depths in more turbid waters, while they have been found deeper at locations with greater water transparency (Samper-Villarreal & Cortés 2020). Nutrient concentrations have been linked to water transparency, as excessive nutrients can cause water to become more turbid. In the Pacific coast of Costa Rica, nutrient concentrations at seagrass locations have been reported to be <2 mmol L⁻¹ for phosphate, <10 mmol L⁻¹ for ammonium, nitrite, and nitrate, and <75 mmol L⁻¹ for silicate (Table 1). However, there are currently no threshold values for

adequate water quality readily accessible for this region. In other regions of the world, seagrass depth range has been used as a bioindicator of water quality, such as Moreton Bay in Australia (Abal & Dennison 1996) and Chesapeake Bay in the USA (Dennison et al. 1993). Early findings indicate the potential to apply seagrass depth range as an indicator of diminished water quality within the ETP.

Seagrasses in the ETP have been found at variable water salinity and temperature, with seagrass presence at salinities ranging between 19 and 35 and at temperatures from 26 to 32°C (Table 1). In a recent aquarium study (Van Barneveld-Pérez 2020), the clover grass *H. baillonii* was collected from the Pacific of Costa Rica and experimentally exposed to hyposaline (15) and hypersaline (35) conditions compared to a control (25). The effects of temperature variability on *H. baillonii* were also assessed, exposing plants to lower (23°C) and higher temperatures (33°C) compared to a control (28°C). In both experiments, plant survival, horizontal rhizome elongation, leaf area, and shoot production were better in control or lower temperature and salinity conditions. In contrast, higher salinities and temperatures led to negative impacts (Van Barneveld-Pérez 2020). These experimental findings could indicate that this species may be better suited to withstand lower saline concentrations and colder water temperatures. However, *H. baillonii* is a very rare species with a fragmented distribution, only found at a limited number of locations. Further studies on salinity and temperature tolerances and thresholds for this and other seagrass species in field conditions in the ETP are recommended, particularly in the face of climate change and El Niño-Southern Oscillation events. For seagrasses in the ETP, only limited *in situ* information is available for pH, dissolved oxygen, chlorophyll, and suspended sediments (Table 1).

Ecosystem services

Seagrass meadows provide a multitude of direct and indirect benefits, which can vary among regions and according to the species present (Nordlund et al. 2016). Seagrasses in the ETP comprise three genera of small seagrasses: *Halodule*, *Halophila*, and *Ruppia*. As part of the TA seagrass bioregion, these seagrass species provide benefits such as serving as a nursery habitat, providing habitat for invertebrates and vertebrates, including fish, providing food for associated species, sediment stabilization, water purification, being useful for compost fertilizer, research, recreation, and tourism (Nordlund et al. 2016). Recent studies show that seagrasses in the ETP serve as a habitat for invertebrates, fish, and sea turtles. Meadows of *H. wrightii*

Table 1. Minimum and maximum reported environmental conditions (mean) where seagrasses have been found in the Eastern Tropical Pacific. Corresponding names for the location numbers are indicated in the legend of Figure 1.

Parameter	Min	Max	Location	Source
Water depth (m)	2	6	4, 6	Samper-Villarreal et al. (2018b), Samper-Villarreal & Cortés (2020)
Water column				
Salinity	19	35	4, 6	Samper-Villarreal et al. (2014, 2018b)
Temperature (°C)	26	32	1, 6	Barquero-Chanto (2018), Samper-Villarreal et al. (2020)
Dissolved oxygen (mg L ⁻¹)	6	8	6	Samper-Villarreal & Cortés (2020)
pH	7	8	6	Barquero-Chanto (2018)
Secchi (m)	0.2	10	5, 6	Barquero-Chanto (2018), Samper-Villarreal et al. (2022a)
Chlorophyll (mg L ⁻¹)	0.6	0.6	1	Samper-Villarreal et al. (2020)
Suspended matter (mg L ⁻¹)	7	7	1	Samper-Villarreal et al. (2020)
Nutrients (mmol L ⁻¹)				
Phosphate	0.1	2	6	Samper-Villarreal & Cortés (2020)
Silicate	4	72	6	Barquero-Chanto (2018)
Ammonium	2	6	5, 6	Barquero-Chanto (2018), Samper-Villarreal et al. (2022a)
Nitrite	1	5	5, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2022a)
Nitrate	0.6	5	5, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2022a)
Sediment grain size (%)				
Gravel (>4 mm)	0.1	28	1, 6	Samper-Villarreal et al. (2014, 2020)
Very fine gravel (4 mm)	1	12	1, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)
Very coarse sand (2 mm)	2	18	5, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2022a)
Coarse sand (1 mm)	2	27	5, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2022a)
Medium sand (0.5 mm)	6	23	1, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)
Fine sand (0.25 mm)	11	38	6	Samper-Villarreal & Cortés (2020)
Very fine sand (0.125 mm)	2	50	5, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2022a)
Silt-clay (>0.062 mm)	0.5	19	1, 6	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)

in El Salvador served as habitat for 22 species of associated macroinvertebrates (Crustacea, Echinodermata, and Mollusca). Many of these are of commercial importance or subsistence and artisanal value for local communities (Ramírez et al. 2017). In Costa Rica, a *H. baillonii* and *R. maritima* meadow on the northern Pacific coast served as habitat for 44 species of associated benthic macrofauna (Cortés 2001). Meanwhile, an *H. baillonii* meadow on the southern Pacific coast had a diversity of macrofauna (Crustacea, Mollusca, Oligochaeta, Nematoda, Nemertea, Ascidiacea, and 17 different families of polychaetes), with seven species reported for the first time for the country (Samper-Villarreal et al. 2014). In the southern Pacific coast of Costa Rica, local communities have indicated seagrass consumption by parrotfish (*Scarus ghobban*) within Golfo Dulce (Samper-Villarreal & Cortés 2020). Sea turtles (*Chelonia mydas agassizii* and *Eretmochelys imbricata*) are highly abundant in meadows and consume seagrasses in this gulf, as supported by recent isotopic evidence (Bessesen & Saborío-R. 2012, Méndez-Salgado et al. 2020, Samper-Villarreal & Cortés 2020). In El Salvador, seagrass meadows are also a sea turtle rest and feeding area (MARN 2010).

Globally, the TA seagrass bioregion and the three small genera found in the ETP are considered to provide lower ecosystem services compared to other bioregions and larger species (Nordlund et al. 2016). Despite their small size, these seagrasses provide many ecosystem services within the ETP. Furthermore, whether seagrasses in the ETP and elsewhere in the world provide many other ecosystem services remains to be seen (Nordlund et al. 2016). Therefore, further research is needed specifically focused on ecosystem services and their valuation within the ETP.

Blue carbon

A seagrass ecosystem service that has been gaining attraction worldwide is the capacity of seagrass meadows for carbon sequestration, thereby aiding in global climate change mitigation. Blue carbon refers to the long-term storage of OC in marine environments, mostly by its burial in the sediment over hundreds to thousands of years (Mateo et al. 1997). Seagrass meadows have the capacity to be long-term carbon sinks, along with mangrove forests and salt marshes (McLeod et al. 2011). Globally, seagrass OC estimates are mostly based on large seagrass species from temperate regions such as *Posidonia*, which are consi-

dered to store higher amounts of OC than smaller and more ephemeral species (Mazarrasa et al. 2021). Given the lack of information previously available on seagrass blue carbon within the ETP region, current global seagrass OC estimates do not include information from ETP seagrasses (Fourqurean et al. 2012). Whether the smaller seagrass species in the TA bioregion can serve as carbon sinks remains a gap in the current global blue carbon knowledge (Nordlund et al. 2016).

There are multiple parameters needed to quantify the OC stored in seagrass meadows, including: 1) total seagrass area (ha); 2) the amount of living above and below ground biomass (g DW m⁻²); 3) the OC (%) stored in seagrass biomass; 4) sediment bulk density (g mL⁻¹); and 5) the OC (%) stored in their associated sediment (Howard et al. 2014). With this information, it is then possible to estimate the various OC pools within seagrass meadows and the total stock (Mg OC ha⁻¹) at a specified depth (Howard et al. 2014). Recent studies have provided the information needed to analyze whether ETP seagrasses can store OC in their biomass and associated sediment (Table 2).

In the ETP, seagrass biomass values have been reported for all three genera found (*Halodule*, *Halophila*, and *Ruppia*). Seagrass biomass is known for multiple locations in Costa Rica: El Jobo and Matapalito (Samper-Villarreal et al. 2020), Bahía Culebra (Cortés 2001), Potrero (Samper-Villarreal et al. 2018b), Sámara (Samper-Villarreal et al. 2022a), and within Golfo Dulce (Sarmiento de Carvalho 2013, Samper-Villarreal et al. 2014, Barquero-Chanto 2018, Samper-Villarreal & Cortés 2020) (Table 2, Fig. 1). ETP biomass values are within the previous biomass ranges reported for these seagrasses (Kantrud 1991, Duarte & Chiscano 1999). Biomass OC percentage has also been directly measured by elemental analysis for *Halodule* and *Halophila* from El Jobo and Matapalito (Samper-Villarreal et al. 2020), Potrero (Samper-Villarreal et al. 2018b), Sámara (Samper-Villarreal et al. 2022a), and within Golfo Dulce (Samper-Villarreal & Cortés 2020). Percentage OC for biomass of these two species in the ETP is reported to range from 26 to 36% (Table 2). In contrast, biomass OC percentage for *Ruppia* within the ETP remains unknown. Seagrass biomass OC pools within the ETP were recently reported from the Pacific coast of Costa Rica at El Jobo, Matapalito (Samper-Villarreal et al. 2020), and Sámara (Samper-Villarreal et al. 2022a) (Fig. 1). With the current information available, above and below ground biomass OC pools in the ETP are estimated to be ≤ 0.2 Mg OC ha⁻¹ (Table 2). Similar to the ETP, seagrass meadows in the Southwestern Atlantic are dominated

by small species of *Halodule*, *Halophila*, and *Ruppia*, and their above-ground biomass OC pools are 0.3 Mg OC ha⁻¹ (Hatje et al. 2023). ETP biomass OC pools are much lower than the global mean of 2.5 Mg OC ha⁻¹ and those estimated from other regions ranging from 0.6 Mg OC ha⁻¹ in the Indo-Pacific to 7.3 Mg OC ha⁻¹ in the Mediterranean (Fourqurean et al. 2012, Howard et al. 2014). ETP biomass OC pools are also lower than in the subtropical Caribbean, where they have been reported to be ≤ 0.6 Mg OC ha⁻¹ for above ground and ≤ 3 Mg OC ha⁻¹ for below-ground pools (Armitage & Fourqurean 2016). Above-ground seagrass biomass OC pools in Australia of 1.9 Mg OC ha⁻¹ (Serrano et al. 2019) are also much higher than in the ETP. Compared to other regions, seagrass biomass in the ETP is low due to communities composed of small colonizing species (Kilminster et al. 2015). Furthermore, this region has seasonal variability in biomass, cover, and species composition (Barquero-Chanto 2018, Samper-Villarreal et al. 2020). Therefore, based on the current information available, the potential for carbon storage in the biomass pool for ETP seagrasses appears to be limited.

In contrast to biomass OC pools, seagrasses appear to store high amounts of OC in their associated sediment in the ETP. Sediment OC percentages in seagrass meadows composed of *Halodule* and *Halophila* with the ETP have now been reported from multiple locations on the Pacific coast of Costa Rica: El Jobo and Matapalito (Samper-Villarreal et al. 2020), Potrero (Samper-Villarreal et al. 2018b), Sámara (Samper-Villarreal et al. 2022a), and within Golfo Dulce (Samper-Villarreal & Cortés 2020) (Fig. 1, Table 2). Sediment bulk densities have also been reported from all of these except at Matapalito. However, sediment percentage OC and bulk density for *Ruppia* meadows in the ETP remain unknown at this time. Sediment OC pools for *Halophila* and *Halodule* meadows in the ETP consist of ≤ 24 Mg OC ha⁻¹_{10 cm} (Table 2). These values are standardized to a limited sediment depth of 10 cm, as only surface sediment cores have been collected in ETP meadows thus far. Surprisingly, this value standardized to 10 cm is similar to values estimated up to 1 m sediment depth in the Indo-Pacific (24 Mg OC ha⁻¹), represents only about half of values in the North Atlantic (49 Mg OC ha⁻¹), are only a third of those from the Northeast Pacific (64 Mg OC ha⁻¹) (Fourqurean et al. 2012, Howard et al. 2014), and just under a fourth of the values reported for small seagrasses in the Southwestern Atlantic (91 Mg OC ha⁻¹) (Hatje et al. 2023). In their top 10 cm, ETP meadows hold higher OC sediment pools than the top

Table 2. Seagrass and sediment mean metrics related to blue carbon calculations in the Eastern Tropical Pacific. AG: above ground. BG: below ground. DW: dry weight. OC: organic carbon. Values <1 are rounded to the nearest decimal, and those >1 are rounded to the nearest integer, except for sediment bulk density. Corresponding names for the location numbers are indicated in the legend of Figure 1. Species refers to the IUCN Red List species code for the seagrasses in the study locations: Hi: *Halophila baillonii*, Hy: *Halodule beaudettei*, Rm: *Ruppia maritima*.

Parameter	Min	Max	Location	Species	Source
Total biomass (g DW m ⁻²)	1	477	3, 6	Hi, Hy, Rm	Cortés (2001), Barquero-Chanto (2018)
AG biomass (g DW m ⁻²)	0.2	97	3, 6	Hi, Hy, Rm	Cortés (2001), Barquero-Chanto (2018)
BG biomass (g DW m ⁻²)	0.6	477	3, 6	Hi, Hy, Rm	Cortés (2001), Barquero-Chanto (2018)
AG biomass OC (%)	32	36	5	Hi, Hy	Samper-Villarreal et al. (2022a)
BG biomass OC (%)	26	34	2, 5	Hi, Hy	Samper-Villarreal et al. (2020, 2022a)
AG biomass OC pool (Mg ha ⁻¹)	0.05	0.2	1, 5	Hi, Hy	Samper-Villarreal et al. (2020, 2022a)
BG biomass OC pool (Mg ha ⁻¹)	0.06	0.2	1, 5	Hi, Hy	Samper-Villarreal et al. (2020, 2022a)
Biomass δ ¹³ C (‰)	-9	-12	2, 6	Hi, Hy	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)
Sediment bulk density (g mL ⁻¹)	0.9	1.4	6	Hi, Hy	Samper-Villarreal & Cortés (2020)
Sediment OC (%)	1	3	1, 6	Hi, Hy	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)
Sediment OC pool (Mg ha ⁻¹) _{10 cm}	16	24	6	Hi, Hy	Samper-Villarreal & Cortés (2020)
Sediment δ ¹³ C (‰)	-19	-28	1, 6	Hi, Hy	Samper-Villarreal & Cortés (2020), Samper-Villarreal et al. (2020)

30 cm in meadows of small seagrasses (*Halodule*, *Halophila*, *Ruppia*, *Zostera*, *Cymodocea*, and *Syringodium*; 12-21 Mg OC ha⁻¹) while they are similar to pools in meadows of large seagrasses (*Amphibolis* and *Posidonia*; 24-29 Mg OC ha⁻¹) in Australia (Mazarrasa et al. 2021). This reveals a high potential for carbon storage in seagrass meadows in the ETP despite their low biomass. Meanwhile, the global mean OC stored in seagrass sediment to 1 m depth is estimated to be 194 Mg OC ha⁻¹ (Fourqurean et al. 2012). OC stored in 1 m of seagrass sediment is 112 Mg OC ha⁻¹ in Australia (Serrano et al. 2019) and can be as high as 372 Mg OC ha⁻¹ in the Mediterranean (Fourqurean et al. 2012). Whether OC can be stored in ETP seagrass sediment for decadal to millennial time periods remains to be clarified. Deeper sediment profiles of at least 1 m depth need to be collected to study OC values at increasing sediment depths and estimate OC sequestration rates and sediment accumulation in ETP meadows, which remain unknown.

The high OC stored in the sediment of ETP meadows could be associated with their habitat characteristics, as they are usually found within calm depositional environments, which favor higher OC storage in seagrass sediment (Mazarrasa et al. 2018). However, meadows formed by larger species in Australia stored higher OC in their sediment than smaller species, irrespective of bioregions and geomorphic setting (Mazarrasa et al. 2021). Meanwhile, in the Southwestern Atlantic, OC pools in meadows composed of small species were about four times lower in subtropical locations compared to

tropical ones (Hatje et al. 2023). This variation was not attributed to latitude but potentially to climate interactions, the characteristics of specific meadows, site geomorphology, and soil formation (Hatje et al. 2023). Isotopic analysis is a useful tool for identifying the sources and flows of carbon (Fry 2006). Stable isotopes can, therefore, provide insight into the factors influencing OC storage in seagrass meadows, as seagrasses can store both seagrass (autochthonous) and non-seagrass (allochthonous) OC in their associated sediment. Carbon isotopic ratios (δ¹³C) of seagrass biomass in the ETP have been reported for *Halodule* and *Halophila* at El Jobo and Matapalito (Samper-Villarreal et al. 2020), Potrero (Samper-Villarreal et al. 2018b), Sámara (Samper-Villarreal et al. 2022a), and Golfo Dulce (Samper-Villarreal & Cortés 2020). In contrast, biomass δ¹³C ratios for *Ruppia* in the ETP remain unknown. Seagrass biomass δ¹³C ratios in ETP seagrasses (Table 2) are similar to the most common seagrass values (Hemminga & Mateo 1996). Seagrass δ¹³C ratios in the ETP do not overlap with the δ¹³C ratios of mangroves in the region (Samper-Villarreal et al. 2018a, Samper-Villarreal & Cortés 2020), proving mangroves to be a useful proxy for isotopic values of terrestrial sources of carbon in isotopic analysis. Therefore, seagrass δ¹³C ratios function as an adequate isotopic source in the ETP to carry out isotope mixing models to assess the contribution of autochthonous OC in the sediment (Fry 2006). Sediment δ¹³C ratios have been reported for meadows dominated by *Halodule* and *Halophila* at El Jobo and Matapalito (Samper-Villarreal et al. 2020), Potrero (Samper-Villarreal et al. 2018b), Sámara (Samper-Villarreal et al. 2022a), and in

Golfo Dulce (Samper-Villarreal & Cortés 2020). Isotopic mixing model analyses ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$) at these sites revealed that seagrasses contribute between 12 to 51% of OC to the associated sediment in seagrass meadows on the Pacific coast of Costa Rica (Samper-Villarreal & Cortés 2020, Samper-Villarreal et al. 2020). Globally, seagrasses are reported to contribute ~50% of the OC stored in the sediment (Kennedy et al. 2010). Contributions of seagrasses to sediment OC in the ETP below 50% could be linked to the small size of seagrass species or environmental conditions. However, more studies at multiple locations are needed to test this notion.

Stressors and loss

Seagrasses are a highly threatened coastal habitat worldwide (Orth et al. 2006, Waycott et al. 2009). Very little is currently known about the distribution of seagrasses in the ETP, yet evidence exists of seagrass loss at Bahía Culebra and El Jobo in Costa Rica. At Bahía Culebra, a meadow of 0.5 ha disappeared in the mid-1990s following a strong storm event (Cortés 2001). At El Jobo, the cause of seagrass loss is not as clear and could be part of natural variability at this site; however, it may also be linked to excessive nutrient loading or sea turtle grazing (Samper-Villarreal et al. 2020). Evidence of herbivory on seagrass leaves has been found at multiple sites on the Pacific coast of Costa Rica (Samper-Villarreal et al. 2014, 2018b), where seagrasses are reportedly consumed by sea turtles and parrot fish (Bessesen & Saborío-R 2012, Samper-Villarreal & Cortés 2020). The seagrass area in El Salvador is also known as a sea turtle rest and feeding area (MARN 2010). However, excessive grazing, particularly by larger grazers such as sea turtles, can lead to diminished seagrass cover and canopy complexity or seagrass loss, as found in Caribbean meadows (Samper-Villarreal et al. 2022b, Christianen et al. 2023).

In El Salvador, seagrasses and biota are threatened by anthropogenic activities, which include resource overexploitation and uncontrolled coastal development (Ramírez et al. 2017). In addition to local anthropogenic stressors, seagrasses are also affected by global impacts such as increasing water temperatures, higher heat wave intensity and length, sea level rise, and coastal erosion. In contrast, seagrass photosynthesis allows them to buffer the negative impacts of ocean acidification (Hall-Spencer et al. 2008, Hendricks et al. 2014). Degradation and loss of seagrass meadows can diminish the ecosystem services they provide. Seagrasses have the potential to shift from carbon sinks

to carbon sources following the loss of living tissue, yet they also can switch back following restoration efforts (Pendleton et al. 2012, Marbà et al. 2015). Given limited seagrass knowledge in the region, the spatial extent and detailed effects of stressors and degradation on ETP seagrasses are currently unknown. Furthermore, there is only one ecological restoration initiative for ETP seagrasses at this time. This initiative started in early 2023 at Bahía Culebra and is currently focused on carrying out a spatial assessment of seagrass presence/absence and seed density, as well as the potential effect of herbivory on seed germination.

In conclusion, recent efforts to better study seagrasses in the ETP have provided key information for this region; however, more studies are urgently needed. Much of the information analyzed here comes from the Pacific coast of Costa Rica. However, the high number of seagrass locations and the increase in recent reports in this country are likely the product of increased seagrass research efforts and should not be interpreted as a reflection of higher seagrass abundance. The dependence on historical records or on recent and geographically aggregated efforts for seagrass mapping in the ETP should also be addressed. Potential ways to improve this include using novel remote sensing methodologies, developing citizen science programs, and building seagrass research capacity in the region. A key issue to address is that OC pools are only reported from surface sediment. Therefore, deeper sediment cores must be analyzed to understand sediment carbon storage over time and provide the first insights into sediment and OC accumulation rates in this region. Seagrasses in the ETP undoubtedly provide many ecosystem services but are highly threatened and have already disappeared from two locations. This review of our current state of knowledge of seagrasses in the ETP highlights the urgent need to strengthen seagrass research capacity, funding, and the number of studies in the broader ETP in years to come to provide a better understanding of seagrass presence and dynamics within the region.

ACKNOWLEDGMENTS

The critically important initial work on seagrass meadows in the Eastern Tropical Pacific, Costa Rica, and more recent collaborations with Dr. Jorge Cortés are greatly appreciated. The author would also like to thank the many students who supported the field and lab work components of seagrass research in Costa Rica. The author's gratitude is extended to the editor and anonymous reviewers for the constructive feedback on ways to improve the original manuscript.

REFERENCES

- Abal, E. & Dennison, W. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research*, 47: 763. doi: 10.1071/MF9960763
- Armitage, A.R. & Fourqurean, J.W. 2016. Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13: 313-321. doi: 10.5194/bg-13-313-2016
- Barquero-Chanto, J.E. 2018. Caracterización y recomendaciones de manejo de una pradera de pastos marinos en playa Colibrí, Golfo Dulce, Costa Rica. M.Sc. Thesis, Universidad Nacional, Heredia.
- Bessesen, B.L. & Saborío-R. G. 2012. Tropical fiord habitats as a year-round resting, breeding, and feeding ground for East Pacific green sea turtles (*Chelonia mydas*) off Costa Rica. *Herpetological Review*, 43: 539-541.
- Christianen, M.J.A., Smulders, F.O.H., Vonk, J.A., Becking, L.E., Bouma, T.J., Engel, S.M., et al. 2023. Seagrass ecosystem multifunctionality under the rise of a flagship marine megaherbivore. *Global Change Biology*, 29: 215-230. doi: 10.1111/gcb.16464
- Cortés, J. 2001. Requiem for an eastern Pacific seagrass bed. *Revista de Biología Tropical*, 4(Suppl.2): 273-278.
- Cortés-Núñez, J., Breedy-Shadid, O., Sánchez-Noguera, C. & Pacheco-Solano, C. 2012. Los ecosistemas marinos del Refugio de Vida Silvestre La Flor y del Corredor Biológico Paso del Istmo, Rivas, Nicaragua. Proyecto investigación marino-costero: asegurando las bases científicas y educativas para la protección y manejo de tortugas marinas en los RVS La Flor y Río Escalante-Chococente. CIMAR, Paso Pacífico, DANIDA, Managua.
- Creed, J.C. & Samper-Villarreal, J. 2019. Clarification of the nomenclature of the seagrass *Halophila baillonii* Ascherson. *Aquatic Botany*, 154: 42-44. doi: 10.1016/j.aquabot.2019.01.002
- Den Hartog, C. 1964. An approach to the taxonomy of the sea-grass genus *Halodule* Endl. (Potamogetonaceae). *Blumea: Biodiversity, Evolution and Biogeography of Plants*, 12: 289-312.
- Den Hartog, C. 1970. *The sea-grasses of the world*. North-Holland Publishing Company, Amsterdam.
- Den Hartog, C., Van Tussenbroek, B.I., Wong, J.G.R., Mercado-Ruaro, P. & Márquez-Guzmán, J.G. 2016. A new *Ruppia* from Mexico: *Ruppia mexicana* n. sp. *Aquatic Botany*, 131: 38-44. doi: 10.1016/j.aquabot.2016.02.005
- Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S., et al. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience*, 43: 86-94. doi: 10.2307/1311969
- Duarte, C.M. & Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. *Aquatic Botany*, 65: 159-174. doi: 10.1016/S0304-3770(99)00038-8
- Duarte, C.M., Kennedy, H., Marbà, N. & Hendriks, I. 2013. Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean & Coastal Management*, 83: 32-38. doi: 10.1016/j.ocecoaman.2011.09.001
- Fiedler, P.C. & Talley, L.D. 2006. Hydrography of the eastern tropical Pacific: A review. *Progress in Oceanography*, 69: 143-180. doi: 10.1016/j.pocean.2006.03.008
- Fiedler, P.C., Mendelssohn, R., Palacios, D.M. & Bograd, S.J. 2013. Pycnocline variations in the Eastern Tropical and North Pacific, 1958-2008. *Journal of Climate*, 26: 583-599. doi: 10.1175/JCLI-D-11-00728.1
- Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., et al. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5: 505-509. doi: 10.1038/ngeo1477
- Fry, B. 2006. *Stable isotope ecology*. Springer, New York.
- Green, E.P. & Short, F.T. 2003. *World atlas of seagrasses*. University of California Press, California.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M. et al. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*, 454: 96-99. doi: 10.1038/nature07051
- Hatje, V., Copertino, M., Patire, V.F., Ovando, X., Ogbuka, J., Johnson, B.J., et al. 2023. Vegetated coastal ecosystems in the Southwestern Atlantic Ocean are an unexploited opportunity for climate change mitigation. *Communications Earth & Environment*, 4: 160. doi: 10.1038/s43247-023-00828-z
- Hemminga, M.A. & Mateo, M.A. 1996. Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. *Marine Ecology Progress Series*, 140: 285-298. doi: 10.3354/meps140285
- Hendriks, I.E., Olsen, Y.S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T.S., et al. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences*, 11: 333-346. doi: 10.5194/bg-11-333-2014

- Hossain, M.S., Bujang, J.S., Zakaria, M.H. & Hashim, M. 2015. The application of remote sensing to seagrass ecosystems: an overview and future research prospects. *International Journal of Remote Sensing*, 36: 61-114. doi: 10.1080/01431161.2014.990649
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M. & Pidgeon, E. 2014. Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses. UNESCO, Paris.
- Kantrud, H.A. 1991. Widgeongrass (*Ruppia maritima* L.): A literature review. *Fish and Wildlife Research* 10. U.S. Department of the Interior Fish and Wildlife Service, Florida.
- Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbà, N., et al. 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24: GB4026. doi: 10.1029/2010GB003848
- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., et al. 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, 534: 97-109. doi: 10.1016/j.scitotenv.2015.04.061
- Kuo, J. & Den Hartog, C. 2001. Seagrass taxonomy and identification key. In: Short, F. & Coles, R. (Eds.). *Global seagrass research methods*. Elsevier Science B.V., Amsterdam, pp. 31-58.
- Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G.A., Mazarrasa, I., Bastyan, G.R., et al. 2015. Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, 103: 296-302. doi: 10.1111/1365-2745.12370
- Ministerio de Medio Ambiente y Recursos Naturales (MARN). 2010. Cuarto Informe al Convenio sobre Diversidad Biológica El Salvador. MARN, San Salvador.
- Mateo, M.A., Romero, J., Pérez, M., Littler, M.M. & Littler, D.S. 1997. Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuarine, Coastal and Shelf Science*, 44: 103-110. doi: 10.1006/ecss.1996.0116
- Mazarrasa, I., Lavery, P., Duarte, C.M., Lafratta, A., Lovelock, C.E., Macreadie, P.I., et al. 2021. Factors determining seagrass blue carbon across bioregions and geomorphologies. *Global Biogeochemical Cycles*, 35: e2021GB006935. doi: 10.1029/2021GB006935
- Mazarrasa, I., Samper-Villarreal, J., Serrano, O., Lavery, P.S., Lovelock, C.E., Marbà, N., et al. 2018. Habitat characteristics provide insights of carbon storage in seagrass meadows. *Marine Pollution Bulletin*, 134: 106-117. doi: 10.1016/j.marpolbul.2018.01.059
- McKenzie, L.J., Nordlund, L.M., Jones, B.L., Cullen-Unsworth, L.C., Roelfsema, C. & Unsworth, R.K.F. 2020. The global distribution of seagrass meadows. *Environmental Research Letters*, 15: 074041. doi: 10.1088/1748-9326/ab7d06
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., et al. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9: 552-560. doi: 10.1890/110004
- Méndez-Salgado, E., Chacón-Chaverri, D., Fonseca, L.G. & Seminoff, J.A. 2020. Trophic ecology of hawksbill turtles (*Eretmochelys imbricata*) in Golfo Dulce, Costa Rica: integrating esophageal lavage and stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analysis. *Latin American Journal of Aquatic Research*, 48: 114-130. doi: 10.3856/vol48-issue1-fulltext-2230
- Nordlund, L.M., Koch, E.W., Barbier, E.B. & Creed, J.C. 2016. Seagrass ecosystem services and their variability across genera and geographical regions. *Plos One*, 11: e0163091. doi: 10.1371/journal.pone.0163091
- Nordlund, L.M., Jackson, E.L., Nakaoka, M., Samper-Villarreal, J., Beca-Carretero, P. & Creed, J.C. 2018. Seagrass ecosystem services - What's next? *Marine Pollution Bulletin*, 134: 145-151. doi: 10.1016/j.marpolbul.2017.09.014
- O'Brien, K.R., Waycott, M., Maxwell, P., Kendrick, G.A., Udy, J.W., Ferguson, A.J.P., et al. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. *Marine Pollution Bulletin*, 134: 166-176. doi: 10.1016/j.marpolbul.2017.09.006
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., et al. 2006. A global crisis for seagrass ecosystems. *BioScience*, 56: 987. doi: 10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2
- Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, W.A., Sifleet, S., et al. 2012. Estimating global "Blue Carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *Plos One*, 7: e43542. doi: 10.1371/journal.pone.0043542
- Phillips, R.C. & Meñez, E.G. 1988. Seagrasses. *Smithsonian Contributions to the Marine Sciences*, 34: 1-104. doi: 10.5479/si.01960768.34

- Ramírez, E., Menjívar, J., Cerén, G., Rivera, A., Henríquez, A. & Liles, M. 2017. Shoalgrass *Halodule wrightii* (Ascherson, 1868) meadows in El Salvador: distribution and associated macroinvertebrates at the estuary complex of Bahía de Jiquilisco. *Latin American Journal of Aquatic Research*, 45: 864-869. doi: 10.3856/vol45-issue4-fulltext-26
- Roelfsema, C.M., Lyons, M., Kovacs, E.M., Maxwell, P., Saunders, M.I., Samper-Villarreal, J., et al. 2014. Multi-temporal mapping of seagrass cover, species and biomass: A semi-automated object based image analysis approach. *Remote Sensing of Environment*, 150: 172-187. doi: 10.1016/j.rse.2014.05.001
- Samper-Villarreal, J. & Cortés, J. 2020. Seagrass characterization on the southern Pacific coast of Costa Rica: History, vegetation, and environment. *Botanica Marina*, 63: 429-438. doi: 10.1515/bot-2020-0022
- Samper-Villarreal, J., Cortés, J. & Polunin, N.V.C. 2018a. Isotopic evidence of subtle nutrient enrichment in mangrove habitats of Golfo Dulce, Costa Rica. *Hydrological Processes*, 32: 1956-1964. doi: 10.1002/hyp.13133
- Samper-Villarreal, J., Moya-Ramírez, J. & Cortés, J. 2022a. First characterization of seagrasses at Sámara Bay, Pacific coast of Costa Rica. *Aquatic Botany*, 178: 103486. doi: 10.1016/j.aquabot.2021.103486
- Samper-Villarreal, J., Moya-Ramírez, J. & Cortés, J. 2022b. Megaherbivore exclusion led to more complex seagrass canopies and increased biomass and sediment C_{org} pools in a tropical meadow. *Frontiers in Marine Science*, 9: 945783. doi: 10.3389/fmars.2022.945783
- Samper-Villarreal, J., van Tussenbroek, B.I. & Cortés, J. 2018c. Seagrasses of Costa Rica: from the mighty Caribbean to the dynamic meadows of the Eastern Tropical Pacific. *Revista de Biología Tropical*, 66: 1. doi: 10.15517/rbt.v66i1.33260
- Samper-Villarreal, J., Bourg, A., Sibaja-Cordero, J.A. & Cortés, J. 2014. Presence of a *Halophila baillonii* Asch. (Hydrocharitaceae) seagrass meadow and associated macrofauna on the Pacific coast of Costa Rica. *Pacific Science*, 68: 435-444. doi: 10.2984/68.3.10
- Samper-Villarreal, J., Rojas-Ortega, G., Vega-Alpizar, J.L. & Cortés, J. 2018b. New sighting of seagrasses in the Eastern Tropical Pacific (Bahía Potrero, Costa Rica). *Aquatic Botany*, 151: 25-29. doi: 10.1016/j.aquabot.2018.07.010
- Samper-Villarreal, J., Cambronero-Bolaños, R., Heidemeyer, M., Mora-Vargas, M. & Mora-Vargas, R. 2020. Characterization of seagrasses at two new locations in the Eastern Tropical Pacific (El Jobo and Matapalito, Costa Rica). *Aquatic Botany*, 165: 103237. doi: 10.1016/j.aquabot.2020.103237
- Sarmento de Carvahlo, M.M. 2013. Análisis descriptivo de las condiciones ambientales y estado de salud de la tortuga negra (*Chelonia mydas agassizii*) en un sitio de forrajeo en el Golfo Dulce, Costa Rica. M.Sc. Thesis, Universidad Nacional, Heredia.
- Saunders, M.I., Leon, J., Phinn, S.R., Callaghan, D.P., O'Brien, K.R., Roelfsema, C.M., et al. 2013. Coastal retreat and improved water quality mitigate losses of seagrass from sea level rise. *Global Change Biology*, 19: 2569-2583. doi: 10.1111/gcb.12218
- Serrano, O., Lovelock, C.E., Atwood, T., Macreadie, P.I., Canto, R., Phinn, S., et al. 2019. Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, 10: 4313. doi: 10.1038/s41467-019-12176-8
- Short, F., Carruthers, T., Dennison, W. & Waycott, M. 2007. Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology*, 350: 3-20. doi: 10.1016/j.jembe.2007.06.012
- Short, F.T., Carruthers, T.J.B., van Tussenbroek, B. & Zieman, J. 2010a. *Halophila baillonii*. The IUCN Red List of Threatened Species, 2010: e.T173382A7004500.
- Short, F.T., Carruthers, T.J.R., van Tussenbroek, B. & Zieman, J. 2010b. *Halodule wrightii*. The IUCN Red List of Threatened Species, 2010: E.T173372A7001725. doi: 10.2305/IUCN.UK.2010-3.RLTS.T173372A7001725.en
- Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., et al. 2011. Extinction risk assessment of the world's seagrass species. *Biological Conservation*, 144: 1961-1971. doi: 10.1016/j.biocon.2011.04.010
- United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) & Short, F.T. 2005. Global distribution of seagrasses UNEP-WCMC, New York. doi: 10.34892/X6R3-D211
- Van Barneveld-Pérez, C.O. 2020. Effects of temperature and salinity on the growth of *Halophila baillonii* in aquaria. M.Sc. Thesis, University of Groningen, Groningen.
- Van Dijk, K., Waycott, M., Biffin, E., Creed, J.C., Albertazzi, F.J. & Samper-Villarreal, J. 2023. Phylogenomic insights into the phylogeography of *Halophila baillonii* Asch. *Diversity*, 15: 111. doi: 10.3390/d15010111

- Van Tussenbroek, B.I., Barba-Santos, M.G., Wong, J.G.R., Van Dijk, K. & Waycott, M. 2010. A guide to the tropical seagrasses of the Western Atlantic. UNAM, Ciudad de México.
- Veettil, B.K., Ward, R.D., Lima, M.D.A.C., Stankovic, M., Hoai, P.N. & Quang, N.X. 2020. Opportunities for seagrass research derived from remote sensing: A review of current methods. *Ecological Indicators*, 117: 106560. doi: 10.1016/j.ecolind.2020.106560
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106: 12377-12381. doi: 10.1073/pnas.0905620106
- Wheeler, M.E., Furman, B.T. & Hall, M.O. 2020. Leaf-tip morphology does not support species status for the seagrass *Halodule beaudettei* in Florida, USA. *Gulf and Caribbean Research*, 31: 31-35. doi: 10.18785/gcr.3101.13

Received: October 31, 2023; Accepted: February 5, 2024