Research article

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Seagrass characterization on the southern Pacific coast of Costa Rica: history, vegetation, and environment

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Abstract: Seagrass conservation and management requires scientific understanding of spatial and temporal variability, information that is currently limited for the Eastern Tropical Pacific (ETP). Here, we analysed seagrass presence based on previous reports, herbarium collections and stakeholder knowledge, combined with field characterization in Golfo Dulce, southern Pacific coast of Costa Rica. Seagrasses were found at multiple locations along a narrow border close to shore and in up to 6 m depth within Golfo Dulce, dating back to 1969. Two seagrass species were found, *Halophila baillonii* and *Halodule beaudettei*. Seagrass biomass values for Golfo Dulce (12.0 ± 8.5 g DW m^{-2}) were lower and water nutrient concentrations were higher than previously reported in the gulf. Shoot density (1513 ± 767 shoots m^{-2}) was similar to previous reports. Stable isotope values in seagrass were −11.3 ± 1.0‰ $\delta^{13}C$ and 1.2 ± 0.9‰ $\delta^{15}N$; while those in sediments were −26.1 ± 1.3 and 2.5 ± 0.9‰. In Golfo Dulce, isotopic values of both seagrass species do not overlap with other known primary producers. Management strategies should aim to minimize known seagrass stressors, protect potential seagrass habitat, and take into account the dynamic life strategies of the two seagrass species found.

Keywords: carbon stocks; Eastern Tropical Pacific; nutrient concentrations; sediment grain size; stable isotopes.

1 Introduction

Seagrass meadows provide a multitude of ecosystem services, such as supporting a complex food web and serving as a nursery habitat for commercially important species (Valentine and Duffy 2006), while also providing coastal protection and mitigation of climate change by carbon sequestration (Nordlund et al. 2018). Anthropogenic impacts threaten seagrasses worldwide and have led to their decline (Orth et al. 2006; Waycott et al. 2009). Seagrass ecosystems are dynamic and their resilience responds to variations at multiple spatial and temporal scales (O'Brien et al. 2018b). Conservation initiatives that successfully protect and manage seagrass meadows are needed (Kenworthy et al. 2006). The Eastern Tropical Pacific (ETP) encompasses the warm waters of the Pacific between Baja California in the north and Ecuador and Peru to the south (Fiedler and Talley 2006). Available scientific information regarding seagrasses in the ETP is limited.

In the ETP, four small, colonizing or opportunistic seagrass species have been reported: *Ruppia maritima*, *Halophila baillonii*, *Halodule beaudettei*, and *Halodule wrightii* (Samper-Villarreal et al. 2018c,d). The taxonomic standing of *H. beaudettei* and *H. wrightii* is currently under study, as it is based on leaf-tip morphology (Phillips 1967; Van Tussenbroek et al. 2010). ETP seagrasses are included in the Tropical Atlantic seagrass bioregion (Short et al. 2007). There are reports of *Phyllospadix* near the northern limit of the ETP, i.e. Baja California in Mexico. This represents the southernmost distribution of this seagrass, which does not grow well at higher temperatures and is not found further south than 24°N (Ramírez-García et al. 2002). *Phyllospadix* is a temperate seagrass which is included in the Temperate North Pacific seagrass bioregion (Short et al. 2007).

Seagrasses in the ETP form discontinuous meadows along the coastline, with few reports overall (Cortés 2001; Phillips and Menez 1988). In recent literature, there are reports of seagrasses only from one location on the Pacific coast of El Salvador (Ramírez et al. 2017), one location in Nicaragua (Cortés-Núñez et al. 2012), and 21 locations in

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Costa Rica (Samper-Villarreal et al. 2014, 2018c,d). Renewed seagrass research efforts in Costa Rica recently reported seagrasses for the first time at 13 locations on the Pacific coast of Costa Rica (Samper-Villarreal et al. 2018d).

Here, we provide a characterization of seagrasses in Golfo Dulce, a gulf on the southern Pacific coast of Costa Rica and, in combination with community knowledge, we aim to answer three key questions for seagrass conservation: 1) What is the spatial distribution of seagrasses in Golfo Dulce?; 2) When were seagrasses first seen in this gulf?; and 3) Do the seagrass species in Golfo Dulce have unique isotopic signatures to discern their role in the food web?

2 Materials and methods

2.1 Study site

Seagrasses were studied in Golfo Dulce, a gulf on the southern Pacific coast of Costa Rica (Figure 1). Golfo Dulce is a 50-km long embayment, 15 km wide, with a shallow 60-m deep entrance and a depth of up to 200 m in the inner portions (Cortés 1990). These characteristics lead to a narrow coastal border with waters that are less than 100 m in depth (Figure 1) and limited circulation (Morales-Ramírez et al. 2015).

2.2 Seagrass presence

A map of seagrass presence in Golfo Dulce was developed by: 1) analysing the available literature reporting seagrass presence; 2) examination of herbarium samples; and 3) interviews with a number of scientists and community stakeholders. We searched in local and international herbaria for seagrass samples previously collected in Golfo Dulce. The Herbario Nacional de Costa Rica (CR) and Herbario de la Escuela de Biología, Universidad de Costa Rica (USJ) were searched locally. International herbaria analysed were the Herbario Nacional de México (MEXU) and the Missouri Botanical Garden Herbarium (MO) (Samper-Villarreal et al. 2018d).

Two community consultation workshops open to all stakeholders were carried out at La Palma (Figure 1) on 21 September 2017 and 12 September 2018. In these workshops, through participatory dynamics, community members identified the locations within Golfo Dulce where they had previously seen seagrasses and the approximate dates on which they were sighted. In total, 34 community members from a wide range of occupations attended the workshops. Their ages ranged from 8 to 67 years old. A number of local colleagues were also interviewed independently regarding the location and dates of previous seagrass sightings in Golfo Dulce (Samper-Villarreal et al. 2018d).

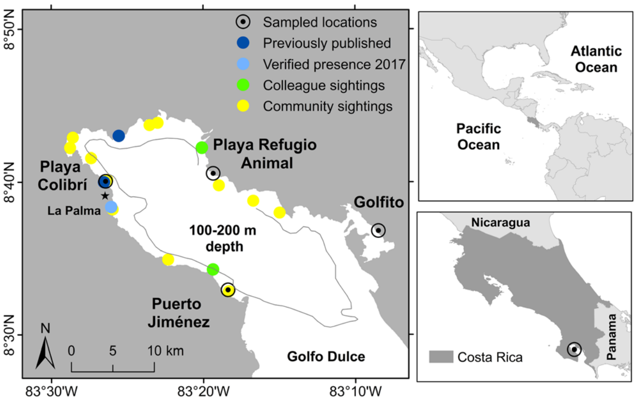

Figure 1: Locations sampled for this study in Golfo Dulce, southern Pacific coast of Costa Rica (Puerto Jiménez, Playa Colibrí, Playa Refugio Animal, and Golfito). Previous published seagrass locations and colleague and community sightings are also shown.

2.3 Characterization of four representative seagrass locations

To provide a preliminary characterization of spatial variation in seagrass locations within Golfo Dulce, four seagrass locations were visited on 18–19 May 2016. These four locations were Puerto Jiménez, Playa Colibrí, Golfito, and Playa Refugio Animal (hereafter referred to as Refugio) (Figure 1). The seagrass species found at each location was recorded and herbarium samples were collected of each species for locations where they had not been previously reported. Samples were deposited at the Herbario de la Escuela de Biología (USJ), Herbario Nacional de Costa Rica (CR), and the State Herbarium of South Australia (AD).

At each location, four seagrass biomass samples were collected using an 11-cm diameter and 15-cm depth PVC corer. Biomass samples were rinsed using a 1-mm mesh, separated into above- (foliar shoots) and below-ground (roots and rhizomes) biomass per species, and placed at 60 °C for a minimum of 48 h or until constant dry weight was obtained. The number of foliar shoots for each seagrass species was counted in each of the biomass cores to calculate shoot density. Leaf area was estimated using ImageJ on photographs of three representative shoots per species in each biomass sample and Leaf Area Index (LAI) was calculated from these values.

The $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures were measured for non-acidified above-ground and below-ground seagrass tissue. For each species and location, the isotopic signatures were measured for four biomass samples of foliar shoots and four rhizome samples. On 22 March 2018, three independent subsurface water samples were collected at Playa Colibrí. The volume of water collected in each sample ranged from 3.7 to 3.9 L. Water samples were filtered using a vacuum pump through glass microfiber filters (Boeco, Hamburg, Germany), which had been previously pre-combusted for 4 h at 550 °C. Used filters were then dried at 60 °C and homogenized for stable isotope analysis. Biomass and filter samples were loaded onto tin capsules for isotopic analysis (Elemental Microanalysis, Okehampton, UK). Total carbon and nitrogen content were also estimated as part of isotopic analysis. Carbon and nitrogen isotopic analyses were carried out at the UC Davis Stable Isotope Facility, California, USA, using an elemental analyser interfaced with a continuous flow isotope ratio mass spectrometer (IRMS). Isotopic ratios are related to international standards, Vienna Pee Dee Belemnite (VPDB) for carbon and air for nitrogen. The standard deviation for $\delta^{13}C$ was 0.2 and 0.3‰ for $\delta^{15}N$ (stableisotopefacility.ucdavis.edu).

2.4 Characterization of environmental parameters

During seagrass characterization in 2016, environmental parameters were measured at each location. Temperature and dissolved oxygen were measured three times at each location using a YSI multiparametric unit (Xylem Inc., New York, USA). Water clarity was assessed by measuring horizontal Secchi disk (Fondriest Environmental, Ohio, USA) distance, as is recommended for shallow seagrass habitats (CARICOMP 2001). Secchi was measured three times at each location. Salinity was measured using a manual refractometer (Atago, Saitama, Japan) from three superficial water samples at each location. Three 50 mL subsuperficial water samples were filtered through a glass microfiber filter, and used for nutrient concentration assessment (Strickland and Parsons 1972) with an autoanalyzer (Lachat Instruments, Milwaukee, USA).

Seagrass sediment samples were collected at each location to measure grain size, stable isotope values, C_{org} and inorganic carbon (C_{inorg}) content. For grain size analysis, four 500 g sediment samples were collected manually. To quantify sediment carbon content and isotope analysis six 20–30 mL sediment samples were collected using a 60 mL plastic syringe. Sediment samples were dried at 60 °C. For grain size analysis, dry 100 g subsamples were sifted using a sieve shaker (Retsch, Haan, Germany) at 90 rpm for 15 min, separating sediment according to particle diameter: > 4, 4, 2, 1, 0.5, 0.25, 0.125, <0.062 mm. Dry bulk density (g mL^{-1}) was estimated for each small sediment sample and homogenized using a mortar and pestle. Sediment carbon content was estimated by Loss on Ignition (LOI) (Heiri et al. 2001). Briefly, for C_{org} quantification dried homogenized sediment samples were placed in pre-weighed porcelain crucibles, re-weighed and combusted at 550 °C in a muffle furnace (Thermo Scientific, Waltham, USA). To quantify C_{inorg}, crucibles were then allowed to cool in a desiccator, reweighed and combusted at 950 °C for an additional 2 h. Crucibles were then cooled and weighed one final time. C_{org} was estimated from organic matter and sedimentary carbon pools were estimated to 10 cm sediment depth (Fourqurean et al. 2012; Howard et al. 2014).

The stable isotope signature was analysed for six sediment samples per location. Sediment $\delta^{15}N$ was estimated from unacidified dried sediment samples which were homogenized using a mortar and pestle. Sediment subsamples (2 mL) were acidified with HCl 10%, dried and homogenized for $\delta^{13}C$ analysis. Sediment samples were loaded onto tin capsules for isotopic analysis.

2.5 Data analysis

Potential variations among locations of seagrass and sediment variables were tested with one-way analyses of variance (ANOVAs), with Tukey post hoc tests. Variation in biomass carbon percentage and $\delta^{13}C$ between species were tested with a Student's test. Contribution of C_{org} sources to seagrass sediments was analysed using mixing models (siar). Potential sources were mean seagrass and particulate organic matter (POM) values found in this study and mean mangrove isotopic values reported for Golfo Dulce: −29.0 ± 1.4‰ $\delta^{13}C$; 3.8 ± 1.4‰ $\delta^{15}N$ (Samper-Villarreal et al. 2018a). Source contribution was the 95% percentile for that source from model outputs. Model residuals were tested for normality and homoscedasticity. Biomass below ground carbon stocks were square root transformed. One unusually high data point was removed as an outlier from Playa Colibrí and another from Puerto Jiménez for sediment $\delta^{13}N$. Non-parametric Kruskal-Wallis analysis was used when needed. To analyse similarity among sites we applied non-metric Multidimensional Scaling (MDS) (Clarke 1993) to data from four samples from each location, using the MASS package, followed by an Analysis of Similarity (ANOSIM) and of Similarity Percentage (SIMPER) (Clarke 1993) using the Vegan package. Parameters used in the MDS for each sample were seagrass LAI, biomass, and above ground $\delta^{15}N$, as well as water depth at which seagrasses were present, and Secchi distance at each site; data for these analyses were not transformed. All analyses were carried out in R v3.5.2 (R Development Core Team 2012).

3 Results

3.1 Seagrass presence

Seagrasses were reported at multiple locations within Golfo Dulce from previous studies, herbarium collections, and colleague reports (Samper-Villarreal et al. 2018d) (Figure 1). We found seagrasses for the first time at three out of the four sites visited in 2016 (Golfito, Refugio, and Puerto Jiménez). From the stakeholder consultation workshops it was clear that local communities were familiar with seagrasses and they easily identified seagrass presence at a multitude of locations, one of which was verified (JSV pers. obs.) in 2017 (Figure 1).

Scientific seagrass sightings date back to 2005 (Didihier Chacón pers. com. JSV). There is an herbarium sample of *H. wrightii* collected in 2009 at Playa Colibrí (MO-2525084). Seagrasses were found at Rincón in 2010 (Samper-Villarreal et al. 2014), and at Playa Colibrí in 2010 and 2011 (Sarmento

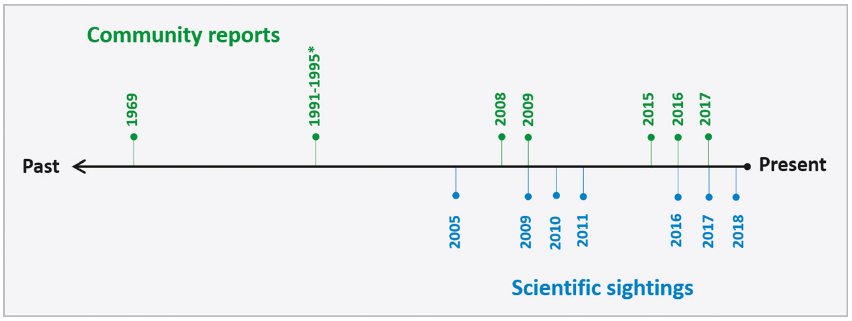

Figure 2: Timeline of scientific sightings and community reports up to 2018 of seagrass presence in Golfo Dulce. *, at some point between 1991 and 1995.

de Carvalho 2013). The local community identified seagrass presence as far back as 1969, with a senior woman at Playa Colibrí and a man in his fifties at Golfito both indicating seagrasses as "*always being there*" (Figure 2).

3.2 Seagrass characterization

Two seagrass species were found during field sampling in Golfo Dulce, *H. baillonii* Ascherson and *H. beaudettei* (Hartog) Hartog. Both species were found at Puerto Jiménez, only *H. beaudettei* at Playa Colibrí, and only *H. baillonii* at Refugio and Golfito (Table 1). Meadow extension at the time of sampling was estimated as ~900 m^2 at Puerto Jiménez; ~100 m^2 at Refugio, and ~100 m^2 at Golfito. The large meadow at Playa Colibrí has been reported to have an extension of ~900,000 m^2 (Sarmento de Carvalho 2013).

Among the four locations sampled, total seagrass biomass was higher at Puerto Jiménez and Playa Colibrí and lower at the other locations ($F = 10.6$, $df = 3$, $p < 0.01$; Table 1). Below-ground biomass followed the same pattern ($F = 26.0$ $df = 3$, $p < 0.01$; Table 1), while above-ground biomass was similar among locations ($F = 2.4$, $df = 3$, $p = 0.1$). Shoot density was higher at Playa Colibrí than the other locations ($F = 3.7$, $df = 3$, $p < 0.01$; Table 1). Leaf Area Index was lower at Puerto Jiménez ($F = 3.5$, $df = 3$, $p = 0.049$; Table 1). There was also variation among locations in seagrass leaf area ($F = 18.3$, $df = 3$, $p < 0.01$), leaf length ($x^2 = 71.1$, $df = 3$, $p < 0.01$), and leaf width ($x^2 = 85.9$, $df = 3$, $p < 0.01$; Table 1).

Mean isotopic values found were –11.3 ± 1.0‰ δ^{13}C and 1.2 ± 0.9‰ δ^{15}N for seagrass; and –19.6 ± 0.05 ^{13}C and 4.7 ± 0.5‰ δ^{15}N for POM (Figure 3). There was no variation in δ^{13}C between seagrass species ($t = 1.1$, $p = 0.27$), while δ^{15}N was slightly enriched for *H. beaudettei* ($t = -2.9$, $p < 0.01$; Figure 3). Tissue δ^{13}C was slightly depleted at Playa Colibrí compared to the other locations while it was slightly enriched at Refugio ($x^2 = 12.9$, $df = 3$, $p < 0.01$; Table 1). Tissue δ^{15}N was lowest at Refugio, highest at Playa Colibrí, and intermediate at the other locations ($F = 24.6$, $df = 3$, $p < 0.01$; Table 1). Seagrass tissue carbon percentage was 32.6 ± 5.4%, with no variation in C_{org} content between species ($t = -2.0$, $p = 0.06$) or between above- and below-ground biomass ($t = 1.6$, $p = 0.12$).

Table 1: Characteristics of seagrasses (mean ± standard deviation) at four locations in Golfo Dulce, southern Pacific coast of Costa Rica, Eastern Tropical Pacific (ETP) (number of samples are in parentheses).

	Puerto Jiménez	Playa Colibrí	Refugio Animal	Golfito
Biomass (g DW m^{-2})				
Halophila baillonii				
Above ground	0.3 ± 0.6 (4)	–	3.0 ± 1.0 (4)	3.6 ± 2.6 (4)
Below ground	1.3 ± 2.3 (4)	–	1.6 ± 0.2 (4)	2.3 ± 1.2 (4)
Total	1.6 ± 3.0 (4)	–	4.6 ± 1.2 (4)	5.9 ± 3.6 (4)
Halodule beaudettei				
Above ground	1.6 ± 0.6 (4)	4.7 ± 0.4 (4)	–	–
Below ground	13.2 ± 5.6 (4)	16.6 ± 6.7 (4)	–	–
Total	14.8 ± 6.0 (4)	21.3 ± 6.7 (4)	–	–
Total seagrass biomass	16.4 ± 6.3 (4)	21.3 ± 6.7 (4)	4.6 ± 1.2 (4)	5.9 ± 3.6 (4)
Shoot density (shoots m^{-2})				
Halophila baillonii	158 ± 316 (4)	–	1316 ± 554 (4)	1132 ± 458 (4)
Halodule beaudettei	1053 ± 412 (4)	2395 ± 891 (4)	–	–
Total density	1211 ± 475 (4)	2395 ± 891 (4)	1316 ± 554 (4)	1132 ± 458 (4)
Leaf length (cm)				
Halophila baillonii	1.0 ± 0.5 (7)	–	1.2 ± 0.2 (48)	1.4 ± 0.5 (41)
Halodule beaudettei	3.1 ± 1.9 (26)	4.5 ± 2.0 (32)	–	–
Leaf width (cm)				
Halophila baillonii	0.55 ± 0.12 (7)	–	0.53 ± 0.06 (48)	0.58 ± 0.12 (41)
Halodule beaudettei	0.06 ± 0.01 (26)	0.08 ± 0.01 (32)	–	–
Leaf area (cm^2 shoot)				
Halophila baillonii	1.2 ± 1.0 (7)	–	2.0 ± 0.4 (48)	2.3 ± 1.2 (41)
Halodule beaudettei	0.4 ± 0.2 (26)	0.9 ± 0.4 (32)	–	–
Leaf area index (m^2 m^{-2})	0.06 ± 0.04 (4)	0.20 ± 0.03 (4)	0.26 ± 0.09 (4)	0.27 ± 0.18 (4)
Isotopes (‰)				
δ^{13}C	−11.4 ± 0.9 (12)	−12.4 ± 0.3 (8)	−10.7 ± 0.5 (8)	−11.4 ± 1.0 (8)
δ^{15}N	1.6 ± 0.6 (12)	3.1 ± 0.5 (8)	0.4 ± 0.6 (8)	1.6 ± 0.8 (8)

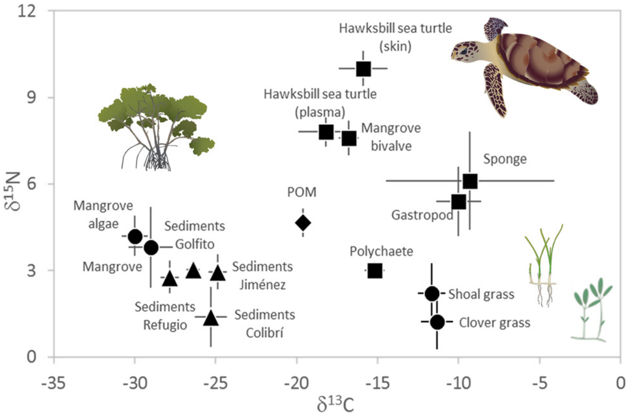

Figure 3: Mean (± standard deviation) isotopic values are presented from this study of seagrass sediments ($n = 6$ at each of four locations) in Golfo Dulce, particulate organic matter (POM, $n = 3$), and two seagrass species: *Halodule beaudettei* ($n = 16$) and *Halophila baillonii* ($n = 20$). Mangrove (*Rhizophora mangle*), mangrove macroalgae (*Bostrychia calliptera)* and mangrove benthic bivalve (*Anadara tuberculosa*), Hawksbill sea turtle (*Eretmochelys imbricata*), sponge (*Mycale* sp.), polychaete (*Amphicteis* sp.) and gastropod (*Cerithium* sp.) isotopic signatures are previously reported values for Golfo Dulce (Méndez-Salgado 2017; Méndez-Salgado et al. 2020; Samper-Villarreal et al. 2018a). Vector images source: Ian Symbols.

3.3 Environmental parameters

Among the four locations, Secchi distance ranged from a mean of 1.2 m at Golfito to 3.7 m at Refugio (Table 2). Seagrasses were found at a shallower water depth at Golfito and deeper at Refugio (Table 2). Dissolved oxygen ranged from 6.1 mg L^{-1} at Golfito to 8.4 mg L^{-1} at Refugio (Table 2). Ammonium, nitrite and nitrate were similar at all locations, while greater variation was noted in silicate and phosphate (Table 2). Salinity was ~30 and temperature ~30 °C at all sites (Table 2).

C_{org} content in seagrass sediments was higher at Refugio and Golfito than at the other locations ($F = 112.7$, $df = 3$, $p < 0.01$; Table 2). C_{inorg} was highest at Golfito and lowest at Refugio ($F = 126.8$, $df = 3$, $p < 0.01$; Table 2). Sediment bulk density was highest at Playa Colibrí and lowest at Golfito ($F = 53.2$, $df = 3$, $p < 0.01$; Table 2). Silt-clay content was higher at Golfito and Refugio and lowest at Playa Colibrí ($F = 63.1$, $df = 3$, $p < 0.01$; Table 2).

Mean stable isotope values for seagrass sediments were −26.1 ± 1.3‰ $\delta^{13}C$ and 2.5 ± 0.9‰ $\delta^{15}N$ (Figure 3). Sediment $\delta^{13}C$ varied among locations ($F = 24.4$, $df = 3$, $p < 0.01$), with slightly enriched values at Puerto Jiménez and Playa Colibrí ($p = 0.71$; Figure 3). Sediment $\delta^{15}N$ was depleted at Playa Colibrí differentiating it from the other locations ($F = 34.0$, $df = 3$, $p < 0.01$; Figure 3). The mean contribution of carbon sources to seagrass sediments was similar at all four locations, with mangroves contributing 78 ± 8%, seagrasses 12 ± 6% and POM 6 ± 5%.

Seagrass locations showed a clustered pattern which revealed dissimilarities among locations ($R = 0.8$, $p < 0.01$; Figure 4). The main variable contributing to the dissimilarity was total seagrass biomass, which contributed 73–79% of the variation between Jiménez and Colibrí, and with either of these sites and Refugio and Golfito. The dissimilarity between Refugio and Golfito was also based on seagrass biomass (27%), along with differentiation regarding Secchi distance (31%) and water depth (26%).

4 Discussion

In dynamic seagrass systems, such as those found in the ETP, data on the spatial and temporal variability of the abundance and presence of seagrasses is essential for adequate conservation and management. Our study provides a first map of seagrass presence in Golfo Dulce – a gulf on the southern Pacific coast of Costa Rica – based on previous reports, community knowledge, and characterization of four seagrass locations. Seagrasses in Golfo Dulce are found within a narrow margin close to the coastline, with marked spatial variability among seagrass locations in seagrass species presence, depth range, and multiple other morphometric parameters. In this gulf, seagrasses have been sighted by the local community as far back as 1969, and by researchers consistently since 2005.

Our findings suggest that suitable seagrass habitat within Golfo Dulce most likely includes all locations close to the coastline to a depth where light availability and sediment characteristics enable seagrass growth. We report seagrass presence at multiple locations within the gulf to a maximum depth of 6 m, associated with fine sediment. This coincides with seagrass locations on the northern Pacific coast of Costa Rica (Samper-Villarreal et al. 2018c, 2020). Light availability is key for seagrasses to thrive and it is negatively affected by anthropogenic factors. Small colonizing seagrasses such as *Halophila* spp. are able to withstand light deprivation for only short periods (O'Brien et al. 2018a). In this study, water clarity was similar to previous reports for two seagrass locations in this gulf (Sarmento de Carvalho 2013; Samper-Villarreal et al. 2014, 2018a). While subtle nutrient loading in Golfo Dulce has been reported (Samper-Villarreal et al. 2018a), we found silicate and phosphate concentrations

Table 2: Environmental and sediment characterization (mean ± standard deviation) at four seagrass locations in Golfo Dulce, southern Pacific coast of Costa Rica.

	Puerto Jiménez	Playa Colibrí	Refugio Animal	Golfito
Environmental variables				
Salinity	30 ± 0 (3)	30 ± 0 (3)	31 ± 0 (3)	30 ± 0 (3)
Dissolved oxygen (mg L^{-1})	7.6 ± 0.1 (3)	8.1 ± 0.1 (3)	8.4 ± 0.1 (3)	6.1 ± 0.7 (3)
Temperature (°C)	29.5 ± 0.0 (3)	30.1 ± 0.0 (3)	29.2 ± 0.0 (3)	29.5 ± 0.1 (3)
Secchi distance (m)	3.3 ± 0.2 (3)	3.4 ± 0.2 (3)	3.7 ± 0.3 (3)	1.2 ± 0.2 (3)
Water depth (m)[a]	3.4 (1)	4.4 (1)	5.7 (1)	3.5 (1)
Water column nutrient concentrations (µmol L^{-1})				
Phosphate	0.14 (1)[b]	0.23 ± 0.09 (3)	1.52 ± 0.90 (2)	0.21 ± 0.04 (3)
Silicate	5.6 ± 1.9 (3)	19.6 ± 21.0 (3)	5.1 ± 2.7 (3)	21.2 ± 15.2 (3)
Ammonium	3.1 ± 0.4 (3)	5.6 ± 4.3 (3)	2.8 ± 0.4 (3)	5.3 ± 3.5 (3)
Nitrite	1.39 ± 0.22 (3)	1.82 ± 0.86 (3)	1.53 ± 0.44 (3)	1.16 ± 0.04 (3)
Nitrate	0.63 ± 0.12 (3)	0.65 (1)[b]	0.79 ± 0.15 (3)	0.60 ± 0.04 (3)
Sediment carbon				
C_{org} (%)	1.3 ± 0.1 (6)	1.2 ± 0.1 (6)	2.0 ± 0.2 (6)	2.7 ± 0.2 (6)
C_{inorg} (%)	2.2 ± 0.0 (6)	2.4 ± 0.1 (6)	1.8 ± 0.1 (6)	2.7 ± 0.1 (6)
Bulk density (g mL^{-1})	1.3 ± 0.1 (6)	1.4 ± 0.1 (6)	1.2 ± 0.1 (6)	0.9 ± 0.1 (6)
C_{org} (Mg ha^{-1})[c]	16.5 ± 1.2 (6)	17.0 ± 1.3 (6)	24.2 ± 1.7 (6)	23.8 ± 2.8 (6)
C_{inorg} (Mg ha^{-1})[c]	28.3 ± 0.9 (6)	34.3 ± 0.7 (6)	21.2 ± 1.2 (6)	23.7 ± 2.2 (6)
Sediment grain size (%)				
Pebbles (>4 mm)	0.7 ± 1.1 (4)	6.0 ± 4.5 (4)	1.4 ± 1.0 (4)	1.4 ± 1.0 (3)
Very fine pebbles (4 mm)	2.1 ± 1.8 (4)	11.6 ± 5.8 (4)	3.2 ± 2.2 (4)	4.2 ± 1.2 (3)
Very coarse sand (2 mm)	3.9 ± 0.8 (4)	18.4 ± 2.4 (4)	6.0 ± 5.9 (4)	14.0 ± 2.6 (3)
Coarse sand (1 mm)	11.0 ± 4.2 (4)	26.6 ± 2.9 (4)	7.6 ± 6.7 (4)	16.7 ± 1.1 (3)
Medium sand (0.5 mm)	22.0 ± 8.0 (4)	23.3 ± 7.7 (4)	12.2 ± 6.8 (4)	22.2 ± 2.2 (3)
Fine sand (0.25 mm)	38.5 ± 3.9 (4)	11.1 ± 4.6 (4)	29.6 ± 8.1 (4)	20.1 ± 2.1 (3)
Very fine sand (0.125 mm)	19.4 ± 5.1 (4)	2.5 ± 1.8 (4)	34.1 ± 14.4 (4)	15.0 ± 0.9 (3)
Silt-clay (>0.062 mm)	2.2± 0.5 (4)	0.5 ± 0.5 (4)	6.0 ± 0.9 (4)	6.5 ± 0.7 (3)

[a] Corrected to maximum depth at High Tide. [b] Only one measured sample because the rest were below the detection level. [c] Estimated for 10 cm sediment depth interval. Number of samples in parentheses.

to lie within the ranges reported. In contrast, ammonium, nitrate, and nitrite were higher than previously reported values. Nutrient enrichment can lead to diminished water clarity, with variations in seagrass depth range and composition used as bioindicators of water quality (Dennison and Abal 1999). In this study, seagrasses were found at shallower depths in the location with the most turbid water, Golfito, which does not appear to be linked to any other environmental variation regarding this location. We therefore highlight that seagrass depth range in Golfo Dulce may be linked to water quality and should be monitored.

Spatial variation among locations is most likely linked to the seagrass species found at each site and their inherent morphometric variation. Seagrass biomass is known to differ among taxa, such as for *Halophila* spp. and *Halodule* spp. (Duarte and Chiscano 1999). Seagrass leaf length, width, and area for both species found were similar to or slightly higher than previous reports from the Pacific of Costa Rica (Samper-Villarreal et al. 2014, 2018c, 2020). Both seagrass species found are colonizing seagrasses and their presence and abundance is dynamic in nature (O'Brien et al. 2018b). The two locations with higher silt-clay content and lower bulk density were the ones where only *H. baillonii* was present; hence sediment characteristics might play a role in species presence or the seagrass species may modify the sediments differently.

Seagrass biomass appears to have declined in Golfo Dulce, yet remains higher than further north on the Pacific coast of Costa Rica. Total seagrass biomass in this study (12.0 ± 8.5 g DW m^{-2}) was lower than two previously reported values for Golfo Dulce, at Rincón and Playa Colibrí (Sarmento de Carvalho 2013; Samper-Villarreal et al. 2014). Biomass was higher than in meadows dominated by these species on the northern Pacific coast (Samper-Villarreal

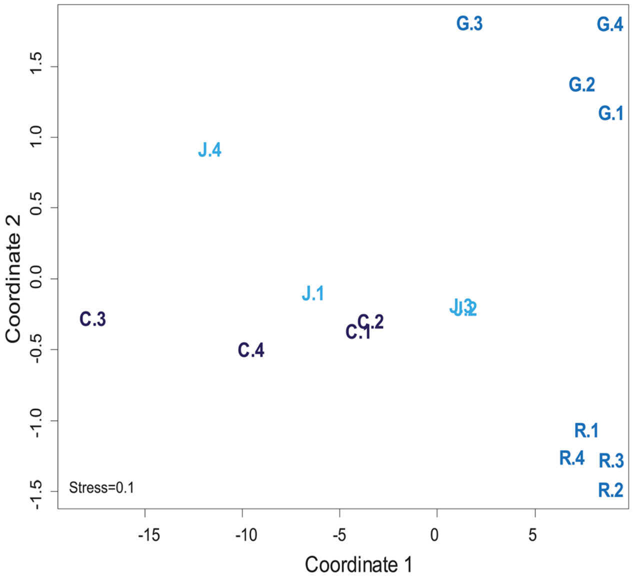

Figure 4: Multidimensional scaling of samples from four seagrass locations within Golfo Dulce: Playa Colibrí (C), Puerto Jiménez (J), Golfito (G), and Refugio Animal (R).

et al. 2018c, 2020). Shoot density (1513 ± 767 shoots m^{-2}) was within reported values for Golfo Dulce (Sarmento de Carvalho 2013; Samper-Villarreal et al. 2014) and two meadows in the northern Pacific (Samper-Villarreal et al. 2020). However, shoot density at Bahía Potrero, another northern meadow, was lower than in our study (Samper-Villarreal et al. 2018c). Shoot density and biomass in a meadow at Bahía Culebra, on the northern coast (Cortés 2001), were much higher than in our study. In contrast to the species found in Golfo Dulce, this northern meadow was dominated by *R. maritima* with only minimal *H. baillonii* presence. This *R. maritima* meadow disappeared in 1996 after a severe storm event (Cortés 2001). Understanding factors influencing variability of seagrasses along the Pacific coast of Costa Rica and the ETP requires further study.

Seagrass biomass δ^{15}N in Golfo Dulce was enriched threefold at Playa Colibrí in comparison to Refugio where it was close to zero. Enriched δ^{15}N values indicate nutrient loading in coastal and marine environments (Costanzo et al. 2001), and was previously used to identify subtle nutrient loading in Golfo Dulce (Samper-Villarreal et al. 2018a). In contrast, sediment δ^{15}N was depleted at Playa Colibrí, while enriched at the other three locations (Figure 3). This variation between biomass and sediment δ^{15}N values may be explained by allochthonous material deposited in seagrass sediments. Another potential confounding factor is that seagrass sediment accretion rates are currently unknown for Golfo Dulce. Accretion rates are ~2 mm yr^{-1} worldwide (Duarte et al. 2013) and can vary among locations and over time (Samper-Villarreal et al. 2018b). It is therefore possible that sediment samples represent different time periods from the seagrass tissue sampled.

A seagrass ecosystem service is carbon sequestration, with silt-clay content known to play a role in sediment carbon stocks (Serrano et al. 2016). In Golfo Dulce, sediment C$_{\text{org}}$ was higher at locations with higher silt-clay content and lower bulk densities. C$_{\text{org}}$ was only slightly lower than the world mean of 2.5% (Fourqurean et al. 2012). Seagrass sediment C$_{\text{org}}$ can be both from allochthonous and autochthonous sources (Kennedy et al. 2010), with multiple techniques currently used to identify carbon sources such as stable isotopes and eDNA (Reef et al. 2017; Samper-Villarreal et al. 2016). The isotopic signatures of mangroves overlap with other terrestrial C3 plants (Lamb et al. 2006; Rodelli et al. 1984), indicating terrestrial/mangrove carbon input to seagrass sediments. In Golfo Dulce seagrasses, sediment C$_{\text{org}}$ was mostly from non-seagrass sources. Sediment δ^{13}C (−26.1 ± 1.3‰) in Golfo Dulce was slightly depleted compared to seagrass locations on the northern Pacific coast of Costa Rica (~ −20‰) (Samper-Villarreal et al. 2018c, 2020), yet all locations appear to have high inputs of allochthonous carbon.

Seagrasses in Golfo Dulce were found to differ isotopically from other potential carbon sources, which may be useful for future food web studies in this gulf. Isotopic signatures of organisms from previous studies in Golfo Dulce varied from seagrass signatures, such as for red mangrove, mangrove macroalgae, mangrove benthic bivalves, sponges, polychaetes, and gastropods (Méndez-Salgado 2017; Méndez-Salgado et al. 2020; Samper-Villarreal et al. 2018a) (Figure 3). Grazing on seagrass leaves has been reported from unknown fish bite marks (Samper-Villarreal et al. 2014) and local communities reported higher presence of parrotfish (*Scarus ghobban*, Scaridae) in seagrass areas. Sea turtle abundance has been linked to seagrass presence in Golfo Dulce (Bessesen and Saborío-R. 2012). The Eastern Pacific green sea turtle (*Chelonia mydas agassizii*) and the Hawksbill sea turtle (*Eretmochelys imbricata*) are reported to consume seagrass in Golfo Dulce (Méndez-Salgado 2017; Sarmento de Carvalho 2013).

Conservation of seagrasses in this gulf is currently lacking or very limited. Golfo Dulce was part of the Southern Pacific Multiple Use Marine Area (AMUM) of Costa Rica, which was established in 1995 (Proyecto Golfos 2012). This gulf was also declared as a Responsible Fishing

Marine Area (AMPR) in 2009 (MAG 2009) and a Hammerhead Shark Sanctuary in 2018 (Castro 2018). However, none of these are considered to be protected areas under the National Conservation Areas System (SINAC) of the Ministry of Environment and Energy (MINAE) of Costa Rica. In contrast, there are multiple terrestrial protected areas surrounding Golfo Dulce (SINAC 2019). Despite these multiple conservation efforts there are currently no clear management or spatial zoning plans including seagrasses in this gulf and no water quality monitoring or waste-water treatment in place.

Given the limited information currently available for spatial and temporal variability of seagrasses in the ETP, our findings provide a basis for seagrass conservation and management initiatives. Taking into account known seagrass stressors, such as diminished water clarity, increased sedimentation, excessive nutrient loading, and boat mooring (Orth et al. 2006), along with the dynamic life strategies of *H. baillonii* and *H. beaudettei*, management strategies should aim towards conservation of potential seagrass habitat.

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