

Presence of a *Halophila baillonii* Asch. (Hydrocharitaceae) seagrass meadow and associated macrofauna on the Pacific coast of Costa Rica

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Abstract

Seagrasses in the Eastern Pacific are mainly confined to temperate and subtropical regions of North America, with limited reports of presence for Central America and Chile. We report a unique monospecific meadow of *Halophila baillonii* for the Eastern Tropical Pacific in Golfo Dulce, southern Pacific coast of Costa Rica. This report constitutes the first sighting of seagrasses from the Pacific coast of Costa Rica since the disappearance of the only reported seagrass meadow of *Ruppia maritima* and *Halophila baillonii* in 1996. Twenty sediment cores (5 cm diam, 15 cm deep) were taken at 10 locations for characterization of seagrass and associated macrofauna, grain size distribution and carbonate analysis. Area of the seagrass meadow was 884 m², foliar shoot density was 4,841 ± 3,433 shoots m⁻², and biomass 30.7 ± 16.3 g DW m⁻². Invertebrate fauna were mainly infaunal, dominated by polychaetes. Seven invertebrate species are new records for Costa Rica and 13 for Golfo Dulce. Further research is needed to elucidate the dynamics and ecological drivers of seagrasses in the Eastern Tropical Pacific.

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Introduction

Seagrasses have a global distribution, with the exception of Antarctica (Short et al. 2001, Green and Short 2003, Larkum et al. 2006). Seagrass meadows are highly productive coastal habitats of great ecological and socio-economic importance (Larkum et al. 2006, McLeod et al. 2011). A diverse fauna is typically associated with seagrass meadows given their high productivity, three-dimensional structure, and accumulated sediment (Hemminga and Duarte 2000, Cortés 2001).

Seagrass meadows are negatively affected by widespread anthropogenic and natural impacts (Orth et al. 2006, Waycott et al. 2009). They have been declining worldwide and are one of the most threatened habitats on the planet (Waycott et al. 2009), a phenomenon exacerbated by an overall lack of charisma (Duarte et al. 2008). Loss of seagrass habitats also affects associated organisms (Hughes et al. 2009).

In the Eastern Pacific, seagrasses are found mainly in temperate and subtropical regions of North America, with limited reports from Central America and Chile (den Hartog 1970, Phillips and Meñez 1988, Davidse et al. 1994, Green and Short 2003). In Costa Rica there are only two seagrass species recorded from the Pacific coast (*Ruppia maritima* and *Halophila baillonii*) (Cortés and Salas 2009). Both species occurred on the North Pacific coast (Bahía Culebra) but were reported to have disappeared after a severe storm in 1996 (Cortés 2001). This previously existing meadow remains the only verified report of seagrasses for the entire Pacific coast of Costa Rica. There have been rare anecdotal reports of seagrasses along the central (Herradura Beach) and southern (Sierpe River) Pacific coast of Costa Rica (Cortés 2001), but seagrass presence at these sites remains unconfirmed. Currently, to the best of our knowledge, no thriving meadows of *H. baillonii* are reported for the Eastern Tropical Pacific (ETP) (see Short et al. 2012).

This study characterizes a seagrass meadow located on the southern Pacific coast of Costa Rica, constituting the first sighting of seagrasses on the Pacific coast of this country since 1996, and the only report of an extant meadow of *H. baillonii* in the ETP. The study aims to provide information on the characteristics of the seagrass meadow, sediment and associated benthic macrofauna.

Materials and Methods

Study Site

Submerged seagrasses were sighted at Rincón de Osa (inner section of Golfo Dulce), on the southern Pacific coast of Costa Rica, and subsequently sampled on October 2010 (8.71698°N, 83.42601°W). Golfo Dulce is a 50 km long and 10–15 km wide tropical fjord-like bay, with a maximum depth of 215 m, and a shallow entrance of 70 m depth (Hebbeln and Cortés 2001, Quesada-Alpízar and Cortés 2006). This leads to calm waters and limited circulation within the bay (Quesada-Alpízar and Morales-Ramírez 2004). A dry season occurs from December to March, and the wet season is from April to November, with transition periods in between. Annual precipitation is between 4,000–5,000 mm yr⁻¹. Mean semidiurnal tidal range within the bay is approximately 3 m (Cortés 1990, IMN 2012).

Meadow characterization

Dimensions of the seagrass meadow were determined by measuring maximum width and length of the meadow at extreme low tide with a 50 m long measuring tape and the use of a Handheld GPS to mark the coordinates of meadow borders (Garmin, GPS map 76 Cx). Water depth was determined at the shallowest and deepest areas with seagrass presence at low tide. Water transparency was determined using a standard Secchi disk at high tide. Two subsurface water samples (10 ml bottles) were collected at high tide directly above the meadow, transported

to the laboratory, and salinity was measured using a handheld refractometer (five subsamples from each bottle). Twenty PVC cores (5 cm diameter x 15 cm depth) were sampled in pairs at 10 random locations within the meadow. From each location, one core was carefully rinsed with freshwater in the laboratory allowing sediment to precipitate between rinsing to avoid sediment loss, then dried at 60 °C for 48 hours or until completely dry. Sediment grain size distribution analysis was carried out following McManus (1988), and carbonate percentage per fraction determined using the weight loss methodology (sensu Seissner and Rogers 1971). Seagrass material was carefully extracted before drying, used for species identification, press dried and deposited in the Herbario Nacional de Costa Rica (CR) and the Escuela de Biología, Universidad de Costa Rica (USJ). Seagrass taxonomic identification was carried out using Phillips and Meñez (1988), Kuo and den Hartog (2001), and Van Tussenbroek et al. (2010).

The second core from each location was preserved in 3 % formaldehyde with Rose Bengal in sea water for invertebrate fauna identification and seagrass biomass determination. Each core was washed with fresh water in the laboratory over a 500 µm sieve to remove sediment, and retained material was preserved in 90 % alcohol until further analysis. Invertebrate fauna from this core was separated and identified to the lowest possible taxon. The de León-Gonzalez et al. (2009) key was used for polychaete identification and *Keen (1971) for mollusks*. Various specimens were deposited in the Museo de Zoología, Universidad de Costa Rica (MZ-UCR).

<< Figure 1 near here >>

Seagrass material was separated into: a) leaves; b) stems; c) rhizomes (including growing tips); and d) roots (Figure 1). Material was dried for 24–48 hours at 60 °C and weighed for biomass determination (g DW m⁻²). Density was determined as the number of foliar shoots (stems with leaves) per core area, and extrapolated to m⁻². When stems with leaves were found

unattached to the rhizome they were still counted as part of the core for density and leaf area purposes. Maximum length and width of attached leaves were measured using a handheld ruler. Leaf area (one-sided) was determined as the sum of leaf blade area per foliar shoot. Leaf area (per shoot) was multiplied by foliar shoot density (shoots m^{-2}) to determine Leaf Area Index (LAI). Epiphytes and fish bites were noted for each leaf (following Valentine and Duffy 2006). Length of each rhizome section was measured using a hand held ruler. Total numbers of foliar shoots, bifurcations, growing tips and nodes per rhizome section were noted.

Relationships between seagrass biomass and each sediment fraction and carbonates were carried out with the Pearson correlation coefficient (r). Invertebrate fauna were also correlated with total sediment content, percentage of each sediment fraction, and carbonates. The degree of variance among samples was expressed using the standard deviation. The statistical program PAST (version 2.01) (Hammer et al. 2001) was used for all statistical analysis.

Results

Seagrass

The meadow was composed exclusively of the clover grass *Halophila baillonii* Asch. (Hydrocharitaceae). Area of the seagrass meadow was 884 m^2 ($\text{length}_{\text{max}} = 52 \text{ m}$; $\text{width}_{\text{max}} = 17 \text{ m}$, not considering irregular meadow borders).. Seagrass foliar shoot density was $4,841 \pm 3,433$ shoots m^{-2} (mean \pm standard deviation (SD), $n = 10$). Minimum density encountered was $1,019$ shoots m^{-2} , and maximum $11,210$ shoots m^{-2} . Seagrass depth range was $1\text{--}2 \text{ m}$ at low tide (corresponding to $4\text{--}5 \text{ m}$ at high tide). Vertical Secchi depth during sampling was $3.8 \pm 0.1 \text{ m}$ (mean \pm SD, $n = 5$). Mean salinity was $19 \pm 0 \text{ ppt}$ and $20 \pm 0 \text{ ppt}$ (\pm SD, $n = 5$ subsamples from each sample).

Mean total seagrass biomass was 30.7 ± 16.3 g DW m⁻² and varied within samples from 10.6 to 56.3 g DW m⁻² (Table 1). Mean biomass per type of tissue decreased as follows: Roots > Rhizomes > Leaves > Stems (Table 1). Biomass per seagrass component revealed a mean below ground (BG) to above ground (AG) ratio (BG:AG) of 3.8 (± 3.3 SD). BG (roots & rhizomes) comprised 72.7 % (range 55–92 %) of total biomass per core, and AG (leaves & stems) 27.3 % (8–45 %). BG and AG biomass both varied within samples, BG: 9.5–40.8 and AG: 1.1–19.8 g DW m⁻² (Table 1). AG showed a weak positive correlation with BG biomass ($r = 0.58$; $p = 0.07$), and with the removal of one outlier (BG = 70.1 mg; AG = 6.4 mg), a positive correlation became clearer ($r = 0.83$; $p < 0.05$). The root:rhizome ratio was 2.1 (± 1.0 SD). Roots represented 64.1 % (49–80 %) of BG biomass per core, and rhizomes 35.9 % (20–51 %). Leaf:stem ratio was 5.2 (± 5.8 SD), leaves represented 74.0 % (23–95 %), and stems 25.9 % (5–77 %) (Table 1).

<< Table 1 near here >>

Overall there were a low number of nodes and bifurcations per rhizome (Table 1). Total number of rhizome sections and growing tips did not show great variation among samples (Table 1). Growing tips were usually encountered in rhizomes with foliar shoots (approximately half of total rhizome sections per sample, see Table 1). Total number of foliar shoots per core was significantly correlated to number of rhizomes per core ($r = 0.95$, $p < 0.05$) (Table 1). Total rhizome length per core showed greater variation among samples (44–270 m m⁻²) (Table 1). Many rhizomes had no foliar shoots present but were no different in color or texture from those with shoots and were included as BG biomass (Table 1). Total number of foliar shoots per core was significantly correlated to number of rhizomes per core ($r = 0.95$, $p < 0.05$). Mean number of leaves per foliar shoot was 3 ± 1 (\pm SD). Leaf length and width were significantly correlated ($r = 0.74$, $p < 0.05$) (Table 1). Minimum measurements of leaf length and width were encountered frequently in immature shoots (very small brown leaves) or leaves affected by herbivory. Mean

LAI was 2.6, but varied greatly from a minimum of 0.1 to a maximum of 6.7. No flowering organs were encountered.

Sediment

Total sediment per core was 271.6 ± 54.8 g (mean \pm SD) and consisted mainly of silt-clay, sand and gravel. Sediment grain size composition analysis revealed mean gravel per core to be 28.4 ± 10.9 % (\pm SD); 15.5 ± 3.0 % coarse sand, 19.0 ± 5.9 % medium sand, 20.0 ± 4.2 % fine sand, and 17.1 ± 10.9 % silt-clay fraction. Mean carbonate content per fraction per core was 4.9 ± 1.9 % (\pm SD), with 9 ± 1 (\pm SD) fractions analyzed for each of the 10 sediment cores. Seagrass BG biomass showed a tendency to decrease when silt-clay increased ($r = -0.62$, $p = 0.058$), and to increase when medium sand increased ($r = 0.62$, $p = 0.056$). No other correlations between BG biomass and other sediments fractions or carbonates were found.

Benthic fauna

A total of 94 individuals of benthic invertebrate macrofauna were encountered. Specimens consisted mainly of polychaetes (68 individuals) in 17 families (most abundant: Orbiniidae, Lumbrineridae, and Spionidae) (Table 2). The rest of the fauna was composed of bivalves (7 ind), nemertines (5 ind), and amphipods (4 ind). Mean number of individuals independent of taxa per core was 9 ± 5 (\pm SD), with a minimum of five individuals per core and a maximum of 21. Invertebrate fauna abundance tended to decrease when total sediment content was higher ($r = -0.55$, $p = 0.10$), and to increase when fine sand was higher ($r = 0.56$, $p = 0.10$). No other correlations between invertebrate abundance and other sediment fractions or carbonates were found. Seven species of invertebrates are new records for Costa Rica and 13 for Golfo Dulce (Table 2).

<< Table 2 near here >>

Discussion

This study reports the presence of seagrasses for the first time in Golfo Dulce, southern Pacific coast of Costa Rica. It is the first report of a monospecific meadow of *H. baillonii* for both coasts of the country, and to our knowledge the only report of a presently existing seagrass meadow of *H. baillonii* for the Eastern Tropical Pacific (ETP) (Short et al. 2012). This report extends the current extant distribution of this seagrass species to the tropical Pacific of Central America.

All reports of *H. baillonii* for the ETP in the last 50 years appear to replicate the report by E.Y. Dawson in 1959 (see den Hartog 1970). The only exception is the 2001 report from Bahía Culebra in Costa Rica (scarce *H. baillonii* within a *R. maritima* meadow) (Cortés 2001). This previous report was confirmed to correspond to *H. baillonii* by analysis of archived material from that location (USJ Herbarium) (pers. obs. J.S.V.). That mixed meadow was the first report of seagrasses for the entire Pacific coast of Costa Rica, but unfortunately it disappeared after a storm in 1996 (Cortés 2001). No further sightings of seagrass, apart from the present study, have been reported for the Pacific coast of Costa Rica since 1996.

Currently *H. baillonii* is categorized as vulnerable under the IUCN Red List and its geographic distribution is limited (Short et al. 2012). It has been reported from less than 10 locations in total, mainly from the Caribbean and Gulf of Mexico, with few reports from Brazil and the Pacific coast of Central America (den Hartog 1970, de Oliveira et al. 1983, Phillips and Meñez 1988, Davidse et al. 1994, Kuo and den Hartog 2001, Van Tussenbroek et al. 2010, Guiry and Guiry 2012, Short et al. 2012). Furthermore, its populations are declining, mostly linked to pollution, diminished water quality and increased coastal development (Short et al. 2011, Short et al. 2012). The species is also no longer found at some previously reported locations such as Dry Tortugas, Brazil, and Bahía Culebra in Costa Rica (Cortés 2001, Short et al. 2012).

Estimated extent of *H. baillonii* in its entire range is less than 2,000 km² (Short et al. 2012). Monospecific meadows of *H. baillonii* range from approximately 0.03 km² to 15km² in Belize (Short et al. 2006). The area of the meadow reported here (884 m²) is less than reported for Belize. Meadow extent in Belize was considered to be limited by freshwater and sediment from rivers during rainy periods (Short et al. 2006). Seagrass area in Golfo Dulce could be limited both by low salinity and increased turbidity towards river discharge areas, and by increasing depth further away from shore, related to the fjord-like characteristics of Golfo Dulce (Hebbeln and Cortés 2001, Quesada-Alpizar and Morales-Ramírez 2004).

The Caribbean and Pacific coasts of Central America present very different conditions for seagrass growth. In the calm waters of the Caribbean, *H. baillonii* can form intermixed meadows with other seagrasses such as *Halophila decipiens*, *Halodule beaudettei* (sometimes identified as *Halodule wrightii*), *Thalassia testudinum*, and even benthic macroalgae (Short et al. 2006, Van Tussenbroek et al. 2010). Tropical seagrass communities from the Eastern Pacific are composed of small-sized genera (*Halodule* and *Halophila*) (den Hartog 1970, Green and Short 2003). Both *H. wrightii* and *H. beaudettei* have been reported for the ETP, and *H. baillonii* was previously found within a meadow of *H. beaudettei* in Panamá (den Hartog 1970, Van Tussenbroek et al. 2010). However, no other seagrass species was encountered in the meadow reported in the present study, which might be indicative of a recently developed meadow.

While the Pacific coast of Mexico and Central America in general has high wave energy and a narrow continental platform, resulting in unfavorable conditions for seagrass development, meadows can thrive in sheltered areas (Cortés 2001, Santamaría-Gallegos et al. 2006). *H. baillonii* is a delicate seagrass species that thrives under diminished light conditions or in sheltered locations, down to 15–30 m depth (den Hartog 1970, Van Tussenbroek et al. 2010, Short et al. 2011). Dominance by *H. baillonii* in turbid or deeper waters might be related to shoot

architecture advantage from its growth form as horizontal leaves elevated from the sediment on an erect stem (Short et al. 2006). The overall calm and turbid waters of Golfo Dulce, particularly in the inner portion, seem well suited to support this seagrass species.

Variation in seagrass density and biomass might reflect variability of environmental factors within the meadow. This study reports *H. baillonii* growing in gravel, sand and fine sediment. Biomass and shoot density variability within the meadow might be related to sediment variability, as this species is not considered to grow well on gravel substrate (den Hartog 1970). Variations of *Halophila* shoot density have been related to their location within the meadows and herbivory (Nakaoka and Aioi 1999), water quality and salinity (Short et al. 2006), as well as seasonal variation (Santamaría-Gallegos et al. 2006). The *H. baillonii* meadow at Golfo Dulce was found at 1–2 m at low tide which equates to depths of at least 4–5 m at high tide, if not deeper at extremely high tides.

Biomass of *H. baillonii* at Golfo Dulce coincided with the low biomass reported for other species of *Halophila* from around the world (Duarte and Chiscano 1999). Below ground (BG) to above ground (AG) biomass ratios were expected to be 1:1 or higher AG for *Halophila* species (Duarte and Chiscano 1999). Surprisingly there was a much higher BG:AG ratio within the meadow, though with high variability among samples. While there were more foliar shoots per sample as the total number of rhizome sections increased, there was an estimated 1:1 ratio of rhizomes with foliar shoots and those without. The rhizome sections that had foliar shoots were almost always found to also have active growing tips, meaning that these shoots were only recently formed and actively growing. The rhizome sections without leaves were identical to those with them, indicating that foliar shoots might have been recently present. A high total length of rhizome sections per core, in particular those without active foliar shoots, helps explain the unexpectedly high BG:AG ratio, though further study is needed. As expected, reproductive

organs were not found in this study (October 2010), since the reproductive period for this species occurs in April and May (Short et al. 2006, Van Tussenbroek et al. 2010).

Halophila baillonii is a small non-leaf replacing pioneer species. Such species of *Halophila* can produce as many as 165 shoots per year, and their rhizomes can grow more than 5m in length per year (Hemminga and Duarte 2000). Algal epiphytes on leaves and hydrozoan epibiota were rare. This could indicate high shoot turnover rates which coincide with a high abundance of rhizome growing tips. Fish herbivory was evident, albeit low, and indicates direct consumption of this seagrass by unknown fish species. Consumption of complete shoots was not evident but it is possible that this might be a factor, and would help clarify the high below ground to above ground biomass ratios and variations in shoot density. Many species of fish and other organisms, such as urchins, gastropods, decapods, and green turtles (*Chelonia mydas*) are known to feed directly on seagrasses (Valentine and Duffy 2006).

Leaf morphology coincided with that reported for the species, with elliptical leaves with an obtuse apex, margin finely serrated, a marked midrib and 3–9 cross veins (den Hartog 1970, Van Tussenbroek et al. 2010) (see Fig.1). While leaf size reported here (1.0 ± 0.4 cm length, and 0.4 ± 0.1 cm width) falls within the reported range of 0.5–2.2 cm length and 0.2–0.6 cm width (den Hartog 1970, Van Tussenbroek et al. 2010), the leaves are at the small end of the range for the species. The reason for their small size remains unclear though it could be related to persistent herbivory and/or light conditions at this site.

The new reports of invertebrates for the area and for the country from the present study are most likely due to lack of sampling in this unique habitat. The assemblage of invertebrates from the Bahía Culebra meadow is dominated by micromollusks, differing from Golfo Dulce, where the fauna is dominated by polychaetes. Cortés (2001) reported 44 species of invertebrates from the meadow in Bahía Culebra, mainly micromollusks (35 spp), polychaetes (6 spp), and

crustaceans (2 spp). The most abundant organisms on *R. maritima* were the gastropod *Alaba supralirata* and the bivalve *Pinna rugosa*. *Strombus gracilior* was found with *H. baillonii* in the deepest sections of the meadow (Cortés 2001). In Golfo Dulce the mollusks were mainly infaunal bivalves.

The results indicate a difference between Bahía Culebra and Golfo Dulce *H. baillonii* systems, possibly related to the way sediments are deposited. The characteristics of these sediments are the main factor influencing the communities of invertebrates (Orth et al. 1984, Little 2000). Heck and Wetstone (1977) found that diversity of invertebrate species is correlated with AG biomass, with dense seagrass meadows providing protection from predators. The BG biomass protects infaunal organisms from predation by epibenthic fishes and crabs (Orth et al. 1984). The high variability of invertebrates among cores might be a result of variations in sediment characteristics and seagrass biomass.

Lack of previous reports of seagrasses in Golfo Dulce evokes the question of whether this species just recently colonized Golfo Dulce. Intensive surveys by one of the authors (JC) in the 1980's never encountered the seagrass. However, further study on seasonal variability and response to environmental changes, as well as distribution of seagrasses within Golfo Dulce is required before assumed recent colonization can be claimed. Lack of seagrass reports in the ETP could be interpreted as the absence of seagrass in the ETP, however, seagrass research in this region has been very limited (Cortés and Salas 2009). There is a need to understand whether seagrasses are continuously colonizing calm shallow waters but are naturally ephemeral or sensitive to environmental variations, as observed at Bahía Culebra (Cortés 2001). The source and method of colonization also require further research, and whether vegetative fragments or seed dispersal is involved is yet to be determined. The importance of seagrass habitats is widely accepted, as is their continued decline worldwide (Orth et al. 2006, Waycott et al. 2009), and

continued research to understand the dynamics and ecological drivers of seagrasses in the Eastern Tropical Pacific is needed.

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Table 1. Mean (\pm SD) biomass (n = 10), leaf length and width (n = 325), leaf area per foliar shoot (n = 95), and rhizome characteristics (n = 10) of *Halophila baillonii*. Golfo Dulce, Costa Rica, 2010.

Component	Subcomponent	Mean	Min-Max	Unit
Biomass	Roots	14.4 \pm 8.7	4.9–29.1	g DW m ⁻²
	Rhizomes	7.4 \pm 3.5	2.2–11.9	g DW m ⁻²
	Leaves	6.8 \pm 6.0	1.1–16.1	g DW m ⁻²
	Stems	2.2 \pm 1.9	0.1–6.7	g DW m ⁻²
	Above ground	9.0 \pm 6.8	1.1–19.8	g DW m ⁻²
	Below ground	21.8 \pm 11.4	9.5–40.8	g DW m ⁻²
	Total	30.7 \pm 16.3	10.6–56.3	g DW m ⁻²
Leaves	Leaf length	1.0 \pm 0.4	0.2–1.6	cm
	Leaf width	0.4 \pm 0.1	0.1–0.5	cm
	Leaf area	1.3 \pm 0.8	0.1–2.8	cm ² foliar shoot ⁻¹
Rhizomes	Total rhizome sections	10 \pm 4	5–17	sections core ⁻¹
	Rhizome sections w/foliar shoots	5 \pm 3	1–8	sections core ⁻¹
	Foliar shoots per rhizome section [•]	1 \pm 1	0–3	shoot section ⁻¹
	Nodes per rhizome section [•]	3 \pm 1	1–7	nodes section ⁻¹
	Bifurcations per rhizome section [•]	0 \pm 1	0–3	bifurcations sections ⁻¹
	Growing tips (GT)	1,631 \pm 1,042	510 - 3 567	GT m ⁻²
	Total rhizome length	164 \pm 73	44 - 270	m m ⁻²

[•] Based on total number of rhizome sections (n=104)

Table 2. Total number of individuals of invertebrate macrofauna per taxon within a monospecific *Halophila baillonii* seagrass meadow in Golfo Dulce, Costa Rica, 2010.

TAXA	INDIVIDUALS
Polychaeta	
<i>Aricidea</i> sp.	2
<i>Axiothella</i> sp. ▲(MZUCR-282-01)	2
Cirratulidae spp. indet.	6
<i>Dorvillea cerasina</i> (Ehlers, 1901) ^{A, D}	2
<i>Exogone</i> (<i>Exogone</i>) cf. <i>verugera</i> (Claparède, 1868) ▲(MZUCR-281-04)	1
<i>Glycera brevicirris</i> Grube, 1870 ^B	1
<i>Hemipodia</i> cf. <i>pustatula</i> Friedrich, 1956 ^B	1
<i>Isolda pulchella</i> Müller in Grube, 1858 ▲ (MZUCR-281-01)	3
<i>Leitoscoloplos mexicanus</i> (Fauchald, 1972) ▲(MZUCR-284-01)	5
<i>Leitoscoloplos panamensis</i> (Monro, 1933)▲(MZUCR-283-01)	6
<i>Linopherus</i> cf. <i>canariensis</i> Langerhans, 1881 ^A	2
<i>Litocorsa</i> sp. ▲ (MZUCR-281-02)	1
<i>Lumbrinerides</i> cf. <i>acuta</i> (Verrill, 1875) ^C	8
<i>Maldane</i> cf. <i>gorgonensis</i> Monro, 1933 ▲ (MZUCR-281-03)	1
<i>Mediomastus</i> cf. <i>californiensis</i> Hartman, 1944 ^{B, C}	2
Paraonidae indet.	2
<i>Paraprionospio pinnata</i> (Ehlers, 1901) ^{B, C}	1
<i>Podarkeopsis brevipalpa</i> Hartmann–Schröder, 1959 ^{B, C}	3
<i>Prionospio lighti</i> Maciolek, 1985 ^C	4
<i>Prionospio pygmaeus</i> Hartman, 1961 ^B	1

	Sabellidae indet.	3
	<i>Spiophanes duplex</i> (Chamberlin, 1919) ^B	4
	<i>Sthenelanelia uniformis</i> Moore, 1910 ^C	2
	Syllidae indet.	1
	<i>Syllis</i> sp. *	2
	<i>Terebellides</i> sp. ^C (MZUCR-281-05)	2
	Oligochaeta indet.	1
	Nemata indet.	2
	Nemertea spp. indet.	5
Mollusca	Donacidae indet. *	1
	Natacidae indet. *	1
	Neritidae: <i>Neritina</i> sp.	2
	Tellinidae: <i>Tellina</i> sp. *	5
	Veneridae: <i>Dosinia</i> sp. *	1
Crustacea	Amphipoda	4
	Decapoda	2
	Ostracoda	1
Asidiacea		1
TOTAL		94

[▲] New report (voucher number at MZ-UCR); ^A Reported in Isla del Coco (Dean *et al.* 2012); ^B Reported in Golfo de Nicoya (Dean 2009), ^C Reported in Golfo Dulce (Dean 2009), ^D Reported in Panama (Dean 2009) * Juvenile specimen.

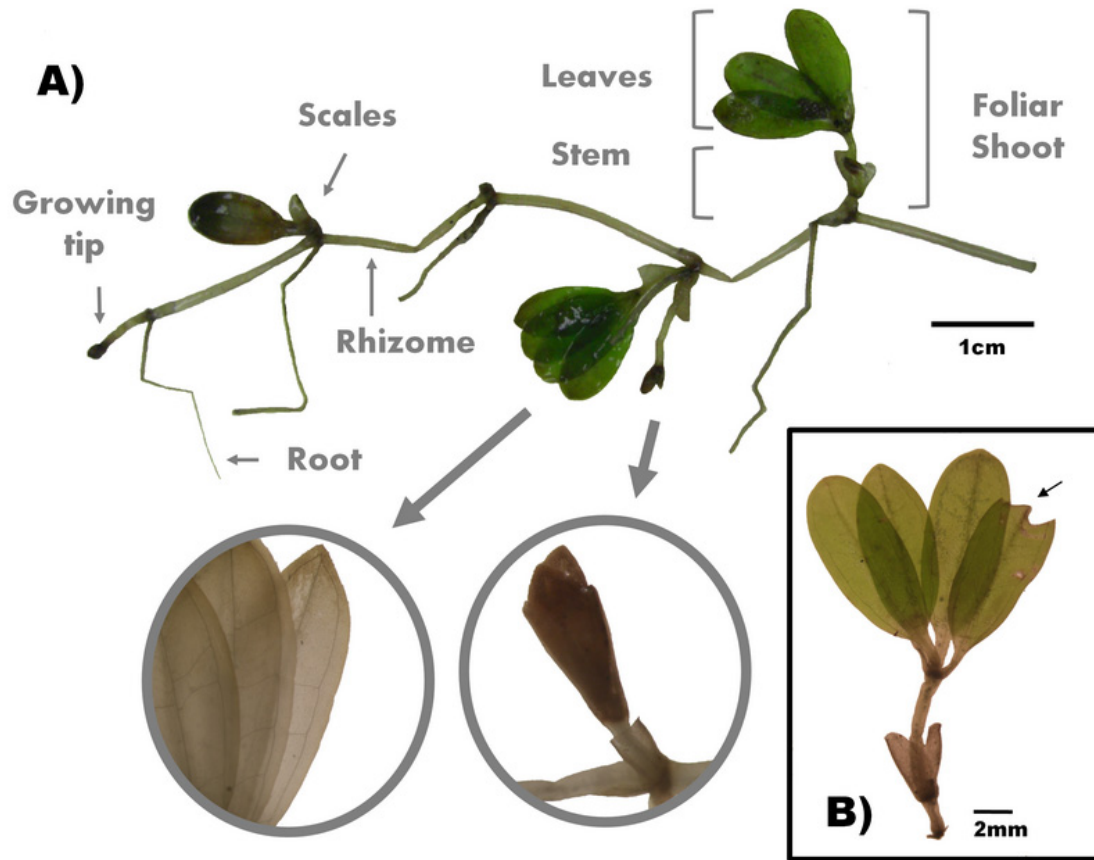


Figure 1. A) Morphological components of *Halophila baillonii* depicting: roots, rhizomes, scales, stems, leaves, foliar shoots, and growing tips. Leaves and new shoots are magnified within the grey circles. B) Foliar shoot with intact leaves and a leaf with two elliptical fish bites (arrow).

Literature Cited

- Cortés, J. 1990. The coral reefs of Golfo Dulce, Costa Rica: distribution and community structure. *Atoll Res. Bull.* 344:1–37.
- . 2001. Requiem for an eastern Pacific seagrass bed. *Rev. Biol. Trop.* 49 (Suppl. 2):273–278.
- Cortés, J., and E. Salas. 2009. Seagrasses. Pages 119–122 (pp. 71–72, Species List) *in* Wehrtmann, I. S., and J. Cortés, eds. *Marine Biodiversity of Costa Rica, Central America*. Springer + Business Media B.V., Berlin.
- Davidse, G., M. S. Sousa, and A. O. Chater (eds). 1994. *Flora Mesoamericana: Vol. 6. Alismataceae a Cyperaceae*. Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.
- de León-González, J. A., J. R. Bastida-Zavela, L. F. Carrera-Parra, M. E. García-Garza, A. Peña-Rivera, S. I. Salazar-Vallejo, and V. Solís-Weiss (eds). 2009. *Poliquetos (Annelida: Polychaeta) de México y América Tropical*. Universidad Autónoma de Nuevo León, México D.F.
- de Oliveira, E. C., J. R. Pirani, and A. M. Giuliatti. 1983. The Brazilian seagrasses. *Aquat. Bot.* 16:251–267.
- Dean, H. K. 2009. Polychaetes and echiurans. Pages 181–191 (pp. 122–159, Species List) *in* Wehrtmann I. S., and J. Cortés, eds. *Marine Biodiversity of Costa Rica, Central America*. Springer + Business Media B.V., Berlin.
- Dean, H. K., J. A. Sibaja-Cordero, and J. Cortés. 2012. Polychaetes (Annelida: Polychaeta) of Parque Nacional Isla del Coco, Pacific Costa Rica. *Pac. Sci.* 66:347–386
- Den Hartog, C. 1970. *The Sea-Grasses of the World*. North-Holland Publishing Comp., Amsterdam-London.

- Duarte, C. M., and C. L. Chiscano. 1999. Seagrass biomass and production: a reassessment. *Aquat. Bot.* 65:159–174.
- Duarte, C. M., W. C. Dennison, R. J. Orth, and T. J. B. Carruthers. 2008. The charisma of coastal ecosystems: addressing the imbalance. *Estuar. Coast.* 31:233–238.
- Green, E. P., and F. T. Short. 2003. *World Atlas of Seagrasses*. UNEP World Conservation Monitoring Centre. University of California. Berkeley.
- Guiry, M. D., and G. M. Guiry. 2012. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. Accessed at <http://www.algaebase.org> on 1 November 2012.
- Hammer, Ø., D. A. T. Harper, and P. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis (Version 2.01. May 2010). *Palaeo. Elec.* 4:1–9.
- Hebbeln, D., and J. Cortés. 2001. Sedimentation in a tropical fjord: Golfo Dulce, Costa Rica. *Geo-Mar. Lett.* 20:142–148.
- Hemminga, M. A., and C. M. Duarte. 2000. *Seagrass Ecology*. Cambridge University. Cambridge.
- Heck, K. L. Jr., and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J. Biogeogr.* 4:135–142.
- Hughes, A. R., S. L. Williams, C. M. Duarte, K. L. Jr. Heck, and M. Waycott. 2009. Associations of concern: declining seagrasses and threatened dependent species. *Front. Ecol. Environ.* 7: 242–246.
- IMN. 2012. Instituto Meteorológico Nacional de Costa Rica. Río Claro Monitoring Station in Golfo Dulce, Costa Rica. Accessed at <http://www.imn.ac.cr> on 1 November 2012.
- Keen, M. 1971. *Sea shells of tropical west America*. Stanford University Press, California. pp. 792–854.

- Kuo, J., and C. den Hartog. 2001. Seagrass taxonomy and identification key. Pages 31–58 in Short, F. T., and R. G. Coles, eds. *Global Seagrass Research Methods*. Elsevier, Amsterdam.
- Kuo, J., and P. G. Wilson. 2008. Nomenclature of the seagrass *Halophila baillonii* Ascherson. *Aquat. Bot.* 88: 178–180.
- Larkum, A. W. D., R. J. Orth, and C. M. Duarte (eds). 2006. *Seagrasses: Biology Ecology and Conservation*. Springer, Dordrecht, The Netherlands.
- Little, C. 2000. *The Biology of Soft Shores and Estuaries*. Oxford Univ. Press, Oxford.
- McManus, J. 1988. Grain size determination and interpretation. Pages 63–85 in Tucker, M., ed. *Techniques in Sedimentology*. Balckwell, Oxford.
- McLeod E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9:552–560
- Nakaoka, M., and K. Aioi. 1999. Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. *Mar. Ecol. Prog. Ser.* 184:97–103.
- Orth, R. J., K. L. Heck, and J. van-Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuar. Coast.* 7:339–350.
- Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Jr. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56:987–996.

- Phillips, R. C., and E. G. Meñez. 1988. Seagrasses. Smithsonian Contributions to the Marine Sciences. Number 34. Smithsonian Institution. Washington D.C., U.S.A.
- Quesada-Alpizar, M. A., and J. Cortés. 2006. Los ecosistemas marinos del Pacífico sur de Costa Rica: Estado del conocimiento y perspectivas de manejo. *Rev. Biol. Trop.* 54 (Suppl. 1):101–145.
- Quesada-Alpizar, M. A., and A. Morales-Ramírez. 2004. Comportamiento de las masas de agua en el Golfo Dulce, Costa Rica durante El Niño (1997 - 1998). *Rev. Biol. Trop.* 52 (Suppl. 2):95–103.
- Santamaría-Gallegos, N. A., R. Riosmena-Rodríguez, and J. L. Sánchez-Lizaso. 2006. Occurrence and seasonality of *Halophila decipiens* Ostenfeld in the Gulf of California. *Aquat. Bot.* 84:363–366.
- Seisser, W. G., and J. Rogers. 1971. An investigation of the suitability of four methods used in routine carbonate analysis of marine sediments. *Deep-Sea Res.* 18:135–139.
- Short, F. T., R. G. Coles, and C. Pergent-Martini. 2001. Global seagrass distribution. Pages 5–30 in Short, F. T., and R.G. Coles, eds. *Global Seagrass Research Methods*. Elsevier Science, Amsterdam.
- Short, F. T., E. Fernandez, A. Vernon, and J. L. Gaeckle. 2006. Occurrence of *Halophila baillonii* meadows in Belize, Central America. *Aquat. Bot.* 85:249–251.
- Short, F. T., T. J. R. Carruthers, B. van Tussenbroek, and J. Zieman. 2010. *Halophila baillonii*. In IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. Accessed at <http://www.iucnredlist.org> on 25 September 2012.
- Short, F. T., B. Polidoro, S. R. Livingstone, K. E. Carpenter, S. Bandeira, J. S. Bujang, H. P. Calumpong, T. G. B. Carruthers, R. G. Coles, W. C. Dennison, P. L. A. Erftemeijer, M. D. Fortes, A. S. Freeman, T. G. Jagtap, A. H. M. Kamal, G. A. Kendrick, W. J. Kenworthy, Y. A. La Nafie, I. M. Nasution, R. J. Orth, A. Prathep, J. C. Sanciangco, B.

- van Tussenbroek, S. G. Vergara, M. Waycott, and J. C. Zieman. 2011. Extinction risk assessment of the world's seagrass species. *Biol. Conserv.* 144:1961–1971.
- Valentine, J. F., and J. E. Duffy. 2006. The central role of grazing in seagrass ecology. Pages 463–501 *in* Larkum, A. W. D., Orth, R. J., and C. M. Duarte, eds. *Seagrasses: Biology Ecology and Conservation*. Springer. Dordrecht, Netherlands.
- Van Tussenbroek, B. I., M. G. Barba Santos, J. G. R. Wong, J. K. van Dijk, and M. Waycott. 2010. *Guía de los Pastos Marinos Tropicales del Atlántico Oeste*. Universidad Nacional Autónoma de México (UNAM). México D.F.
- Waycott, M., C. M. Duarte, T. J. B. Carruthers, T. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Jr. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. USA.* 106:12377–12381.