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Seagrasses of Costa Rica: from the mighty Caribbean to the dynamic meadows of the Eastern Tropical Pacific

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Abstract: Seagrass meadows are declining worldwide, mostly attributed to anthropogenic disturbances. Understanding the dynamics of these meadows is urgent in order to establish adequate management and conservation strategies. Here, we analyzed the current knowledge on the seagrass meadows in the Caribbean and Pacific coasts of Costa Rica, Central America. Current knowledge was based on literature searches, herbarium collections, informal interviews, and personal observations. We report a total of five genera and seven species for Costa Rica: *Thalassia testudinum*, *Syringodium filiforme*, *Halophila decipiens*, *Halophila baillonis*, *Halodule wrightii*, *Halodule beaudettei*, and *Ruppia maritima*. Six species are reported for the Caribbean, and four species for the Pacific. *Thalassia testudinum*, *S. filiforme*, and *H. decipiens* have only been reported for the Caribbean. *Halodule beaudettei* has only been reported for the Pacific coast. *Halophila baillonis*, *H. wrightii* and *R. maritima* have been reported for both coasts. Seagrasses were found at a total of 31 locations in Costa Rica, most from the Pacific coast; 16 of which are reported here for the first time. Seagrass meadows from both coasts are vastly different. Along the Caribbean coast, meadows are often dominated by the robust *T. testudinum*, they are extensive and stable, persisting for decades. In contrast, the meadows along the Pacific coast are more dynamic and are dominated by pioneer and smaller ephemeral species, such as *H. baillonis* and *H. beaudettei*. The number of studies on Costa Rican seagrasses is scarce but has been increasing over time, and mostly concern taxonomic reports and basic descriptions of the dynamics of *T. testudinum* meadows from the Caribbean. Research, conservation and management efforts on Costa Rican seagrass meadows would benefit from continued monitoring and research on associated fauna and flora, incorporating ecosystem resilience and services. Rev. Biol. Trop. 66(Suppl. 1): S53-S65. Epub 2018 April 01.

Key words: Seagrass meadows, coastal wetlands, Eastern Tropical Pacific, Caribbean, Central America, inventory.

Costa Rica is a small country in Central America with 51 000 km^2 total land area (Cortés & Wehrtmann, 2009). The general conditions for seagrass meadows vary greatly between the Caribbean and Pacific coasts, despite both coasts being only 120 - 285 km apart. The Pacific coast is very irregular, with a length of 1 254 km, has a ~3 m tidal range, and hosts a wide variety of habitats (Cortés, 2016a). Meanwhile, the Caribbean coast a length of 212 km with more regular geomorphology, and a much smaller tidal range of approximately 0.5 m (Cortés, 2016b). Costa Rica hosts 3.5 % of the worlds' marine biodiversity (Wehrtmann, Cortés, & Echeverría-Sáenz, 2009), which includes the species associated with seagrass meadows on both coasts (Cortés & Salas, 2009).

Seagrass meadows are important marine habitats that are found along coastlines around the world (Hemminga & Duarte, 2000). Seagrasses are an ecological group of flowering

plants that thrive in saline to brackish waters, and there are between 60 and 72 species of seagrass worldwide (Den Hartog & Kuo, 2006; Short et al., 2011). These plants are the foundation species of diverse coastal ecosystems in shallow waters, with a multitude of associated organisms, providing a plethora of ecosystem services, such as nursery habitat, nutrient recycling, carbon sequestration, sediment deposition, and coastal protection (Nordlund, Koch, Barbier, & Creed, 2016).

Seagrass meadows are declining worldwide (Waycott et al., 2009), including the Caribbean region (Van Tussenbroek et al., 2014). This decline has been strongly linked to anthropogenic activity, mainly nutrient enrichment, increased sedimentation, and light reduction (Orth, Carruthers, Dennison, Duarte, Fourqurean, Heck, et al., 2006; Waycott et al., 2009). Conservation and management initiatives that aim to preserve the functions and presence of seagrass meadows need to have a strong basis on scientific knowledge, including the location and spatial area of seagrass meadows. Presence of seagrass meadows has been acknowledged for many years in Costa Rica; particularly in the Caribbean (Cortés & Salas, 2009). Here, we present recent additions to the reported species and locations of seagrasses for Costa Rica. We analyze previous research efforts on Costa Rican seagrass meadows, and identify key areas for further study.

MATERIALS AND METHODS

Information for this study was gathered by searching google scholar for "Costa Rica + seagrass", "Eastern Tropical Pacific + seagrass", and in Spanish "pastos marinos + Costa Rica", "fanerógamas + Costa Rica". Local library databases were also searched for these terms, and for university thesis, as was the Revista de Biología Tropical online search engine (available at: revistas.ucr.ac.cr). References related to seagrass or seagrass habitat research in Costa Rican coasts were selected for further analyses.

Multiple herbarium collections were searched for Costa Rican seagrass specimens using the different genus and species as keywords. Herbarium specimens from the Herbario Nacional de Costa Rica (CR) and Herbario de la Escuela de Biología, Universidad de Costa Rica (USJ) were photographed and analysed in person. Specimens from the Herbario Nacional de México, Universidad Nacional Autónoma de México (MEXU), were searched digitally online and detailed high resolution photographs of each specimen were assessed (datosabiertos.unam.mx). The information from the specimens at the Missouri Botanical Garden Herbarium (MO) was searched on their online Tropicos database (tropicos.org). Information was also included in this analysis from new herbarium samples collected in recent years that have been recently deposited at CR, USJ and the State Herbarium of South Australia (AD) and have yet to be assigned herbarium identification numbers.

Informal interviews were conducted with local contacts that responded positively when asked if they had ever seen seagrasses on the Pacific coast of Costa Rica. Interviewees included researchers, field technicians and research assistants at the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) at the Universidad de Costa Rica (UCR), students at the Escuela de Biología, UCR, Non-Government Organization workers, conservation area government workers, divers and local coastal residents. During these interviews, they were asked to identify the species from a plate with pictures of various local seagrass species or to describe details of the spotted plants including the location and date of the sighting. A map was used to identify key locations whenever possible. Maps with identified seagrass locations or names of locations provided during interviews and herbarium samples with only location name were then used to extract approximate coordinates for each meadow using Google Earth (7.1.7.2606). Additional localities have been observed directly by the authors.

RESULTS

Seven seagrass species are reported for Costa Rica. Six species are reported for the Caribbean, and four species for the Pacific (see taxonomic considerations for some seagrass species in the discussion). Three species are only present in the Caribbean, and one species is only reported for the Pacific coast of Costa Rica. Three species occur along both coasts (Table 1). Most species are classified as Least Concern in the IUCN Red List; except for *Halophila baillonis* which is listed as Vulnerable, and *Halodule beaudettei* is classified as Data Deficient, mainly due to uncertainties concerning its taxonomical status (Table 1).

Seagrasses occur at 31 locations, of which 16 are reported for the first time in this study (Fig. 1, Table 2). These new records consist of herbarium samples collected previously (four locations), personal communications during the informal interviews in this study (seven locations), and recent new sightings by the authors (five locations) (Table 2). Of the locations where seagrasses have been found previously (Table 2), we can confidently say, from recent observations, that seagrasses are present on the Pacific coast at Bahía Jobo, Bahía Culebra, Bahía Potrero, Isla Chora, Punta Leona, Parque Nacional Marino Ballena, and most extensively at Golfo Dulce. In the Caribbean, seagrasses have been observed recently at Isla Uvita, Parque Nacional Cahuita (hereafter PNC), Puerto Viejo, and Refugio Nacional de Vida Silvestre Gandoca-Manzanillo (hereafter RGM). Based on the current information, total seagrass area for Costa Rica is estimated as 1 328 384 m^2 (132.8 ha), most on the Pacific coast.

Seagrasses have been found at ten locations in the Caribbean, with three locations reported in this study for the first time (Table 2). Seagrass presence is limited to sheltered areas near the port city of Limón and in coral reef lagoons further south at PNC and the

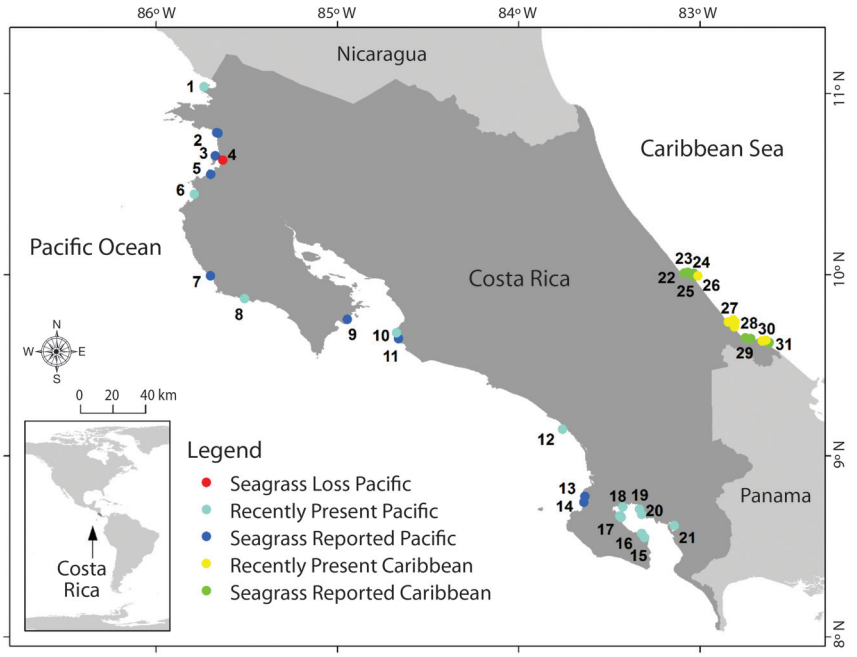

Fig. 1. Seagrass presence on the Pacific and Caribbean coasts of Costa Rica, Central America. Numbers refer to individual seagrass locations (see Table 2). Seagrass categories: "Seagrass Loss" refers to a meadow where seagrasses were lost and have not yet recovered. "Recently Present" refers to meadows which have seen at that location within the current decade. "Reported Seagrass" refers for locations for which there are only older herbarium samples or personal communications.

TABLE 1
Seagrass species reported for each coast of Costa Rica. IUCN Red List and population trends from Short et al. (2011). Pop = Population Trend Worldwide

Species	Reports in the Caribbean	Reports in the Pacific
Hydrocharitaceae		
Thalassia testudinum IUCN: Least Concern Pop: Stable	Dawson, 1962; Den Hartog, 1970; Wellington, 1974; Risk, Murillo, & Cortés, 1980; Gómez, 1984; Cortés & Guzmán, 1985; Cortés & Risk, 1985; Phillips & Meñez, 1988; Cortés et al., 1992; Davidse, Sousa, & Chater, 1994; Cortés & Jiménez, 2003; Crow, 2003b; Green & Short, 2003; Cortés & Salas, 2009; Cortés et al., 2010; Krupp, 2006; Krupp, Cortés, & Wolff, 2009; Nielsen Muñoz, 2006, 2007; Paynter, Cortés, & Engels, 2001; Van Tussenbroek et al., 2010; Van Tussenbroek et al., 2014;	None
Halophila decipiens IUCN: Least Concern Pop: Stable	Gómez, 1984; Phillips & Meñez, 1988; Davidse et al., 1994; Crow, 2003b; Green & Short, 2003; Krupp, 2006; Nielsen Muñoz, 2006, 2007; Nielsen-Muñoz & Cortés, 2008; Cortés & Salas, 2009; Van Tussenbroek et al., 2010	None
Halophila baillonis IUCN: Vulnerable Pop: Decreasing	Dawson, 1962; Wellington, 1974; Gómez, 1984; Phillips & Meñez, 1988; Crow, 2003b	Gómez, 1984; Phillips & Meñez, 1988; Cortés, 2001; Green & Short, 2003; Krupp, 2006; Nielsen Muñoz, 2006, 2007; Cortés & Salas, 2009; Van Tussenbroek et al., 2010 Bessesen & Saborío-R., 2012; Sarmento de Carvalho, 2013; Samper-Villarreal et al., 2014
Cymodoceaceae		
Syringodium filiforme IUCN: Least Concern Pop: Stable	Dawson, 1962; Wellington, 1974; Gómez, 1984; Cortés & Guzmán, 1985; Phillips & Meñez, 1988; Cortés et al., 1992; Davidse et al., 1994; Cortés & Jiménez, 2003; Green & Short, 2003; Hammel, 2003; Cortés & Salas, 2009; Krupp, 2006; Nielsen Muñoz, 2006, 2007; Krupp et al., 2009; Van Tussenbroek et al., 2010	None
Halodule wrightii IUCN: Least Concern Pop: Increasing	Gómez, 1984; Phillips & Meñez, 1988; Cortés et al., 1992; Davidse et al., 1994; Green & Short, 2003; Hammel, 2003; Krupp, 2006; Nielsen Muñoz, 2006, 2007; Cortés & Salas, 2009; Van Tussenbroek et al., 2010	Phillips & Meñez, 1988; Green & Short, 2003; Van Tussenbroek et al., 2010
Halodule beaudettei IUCN: Data Deficient Pop: Unkown:	None	Sarmento de Carvalho, 2013
Ruppiaceae		
Ruppia maritima IUCN: Least Concern Pop: Stable	Dawson, 1962; Gómez, 1984; Davidse et al., 1994; Cortés & Salas, 2009; Van Tussenbroek et al., 2010	Gómez, 1984; Phillips & Menez, 1988; Davidse et al., 1994; Cortés, 2001; Crow, 2003a; Nielsen Muñoz, 2006, 2007; Cortés & Salas, 2009; Van Tussenbroek et al., 2010

TABLE 2

Seagrass locations reported for the Caribbean and Pacific coasts of Costa Rica, with the date sighted, species present, estimated extension, verification evidence and cited publications. AD = State Herbarium of South Australia; CR = Herbario Nacional de Costa Rica; MEXU = Herbario Nacional de México, Universidad Nacional Autónoma de México; JS = Jimena Samper personal code; MO = Missouri Botanical Garden; USJ = Herbario de la Escuela de Biología, Universidad de Costa Rica. TBA = to be assigned. nk = Not known

Location number (Fig. 1)	Location	Species Herbarium collections	Extension (m^2)	Water column depth	References
Pacific	**Northern**				
1	Bahía Jobo [1]	*Halophila baillonis*	60 000	0.5 - 2 m	This study
2	Playa Naranjo, Parque Nacional Santa Rosa	*Ruppia maritima* MO-Grayum #5131; CR-119424	nk	nk	Crow, 2003a
3	Bahía Huevo [2]	c.f. *Ruppia maritima*	nk	1 - 8 m	This study
4	Bahía Culebra [3]	*Ruppia maritima** *Halophila baillonis* USJ-005824	<100 - 5 000	< 2 m	Cortés, 2001; Crow, 2003b
5	Playas del Coco	*Ruppia maritima* USJ-7228	nk	nk	This study
6	Bahía Potrero [4]	*Halodule beaudettei* CR-TBA *Halophila baillonis* CR-TBA	nk	6 m	This study
7	Estero de Ostional	*Ruppia maritima* MEXU-546253	nk	0 m	This study
8	Isla Chora, Sámara [5]	*Halophila baillonis*	~ 100	3 m	This study
9	Bahía Curú [2]	*Halophila baillonis*	nk	1 - 8 m	This study
	Central				
10	Reserva Biológica de Punta Leona	Unkown	nk	0 - 3.5 m	Myers et al., 2011
11	Herradura	Unkown	nk	nk	Cortés, 2001
12	Parque Nacional Marino Ballena	*Ruppia maritima*	nk	nk	This study
	Southern				
13	Mouth of Río Siepre	*Halophila baillonis* MEXU-1249952	nk	0.01 - 0.2 m	Cortés, 2001
14	Playa Ganado, Bahía Drake	Unkown	nk	nk	BIOMARCC-SINAC-GIZ, 2012
15	Puerto Jiménez, Golfo Dulce [6]	*Halodule beaudettei* AD-TBA, CR-TBA, USJ-TBA *Halophila baillonis* AD-TBA, CR-TBA, USJ-TBA	~ 900	2 - 3 m	This study
16	Playa Ñeques, Golfo Dulce [7]	c.f. *Halophila baillonis*	nk	nk	This study
17	Playa Colobrí, Golfo Dulce [8,9]	*Halodule beaudettei* USJ-101555, CR-TBA, AD-TBA, CR-TBA, USJ-TBA *Halodule wrightii* MO-2525084 *Halophila baillonis* USJ-101556, CR-TBA, AD-TBA	(> 400) 900 000	5 - 6 m	Bessesen & Saborío-R., 2012; Sarmento de Carvalho, 2013; Sarmento et al., 2016
18	Rincón, Golfo Dulce [10]	*Halophila baillonis* USJ-101557, CR-TBA	884	4 - 5 m	Samper-Villarreal et al., 2014
19	Piedras Blancas, Golfo Dulce [7]	c.f. *Halophila baillonis*	nk	nk	This study
20	Playa Animal, Golfo Dulce [8]	*Halophila baillonis* AD-TBA, CR-TBA, USJ-TBA	~ 100	4 - 5 m	This study
21	Golfito, Golfo Dulce [8]	*Halophila baillonis* AD-TBA, CR-TBA, USJ-TBA	~ 1 000	< 1 m	This study

TABLE 2 (Continued)

Location number (Fig. 1)	Location	Species Herbarium collections	Extension (m^2)	Water column depth	References
Caribbean	**Southern**				
22	Moín	*Ruppia maritima* MO-1936778	nk	nk	Dawson, 1962
23	Portete	*Thalassia testudinum* *Halophila decipiens* USJ-038574, USJ-038575, USJ-038576 *Halophila baillonis*	nk	1 m	Dawson, 1962; Cortés & Guzmán, 1985; Cortés & Jiménez, 2003; Crow, 2003b
24	Piuta [2]	*Thalassia testudinum*	nk	< 2 m	This study
25	Isla Uvita [2,8]	*Thalassia testudinum* *Halophila decipiens* USJ-TBA	400	8 m	Cortés & Guzmán, 1985
26	Puerto Limón	*Thalassia testudinum* CR-66687	nk	nk	Dawson, 1962
27	Cahuita	*Thalassia testudinum* MO-A Lot #1255, MEXU-366392, CR-062284, CR-274353, CR-TBA, USJ-017357, USJ-031104, USJ-031105, USJ-031106, USJ-037843, USJ-024515, CR-198189, USJ-102076, USJ-92778, USJ-92779 *Syringodium filiforme* MO-A Lot #1258, MEXU-366595, CR-50.020, CR-138191, CR-167852, USJ-017312, USJ-037843, USJ-104913, USJ-104919, USJ-104920, USJ-104921, USJ-92780 *Halodule wrightii* MO- 2525084, MEXU-366577, MEXU-366593, AD-TBA, USJ-TBA *Halophila decipiens* MO-684710, MEXU-366594, CR-138146, USJ-88569, USJ-85511	200 000	0 - 7 m	Dawson, 1962; Wellington, 1974; Risk et al., 1980; Cortés & Guzmán, 1985; Cortés & Risk, 1985; Cortés, 1998; Cortés & Jiménez, 2003; Crow, 2003b; Fonseca et al., 2007; Wetzer & Bruce, 1999
28	Puerto Viejo	*Thalassia testudinum* CR-87408, CR-257304	nk	nk	This study
29	Cocles	*Thalassia testudinum*	Small patches	nk	Fernández & Alvarado, 2004
30	Manzanillo	*Thalassia testudinum* CR-273678 *Syringodium filiforme* CR-273679	160 000	1 - 5 m	Cortés & Guzmán, 1985; Chacón, McLarney, Ampie, & Venegas, 1996; Krupp et al., 2009
31	Punta Mona	*Thalassia testudinum* CR-93991	nk	nk	This study

Notes: 1. Pers. com. and specimen sampled by M. Heidemeyer. 2. Pers. com. Eleazar Ruiz, 2016. 3. This meadow disappeared in the mid-1990s; there is photographic evidence. 4. Unpublished data JSV & pers. com. Mauricio Méndez, Javier Espinach, Gustavo Rojas-Ortega sighted 2015 with photographic evidence, 2016. 5. Pers. com. and photographs from Giovanni Bassey, Alvaro Segura y Mauricio Méndez, 2016. 6. Unpublished data JSV & JCN & pers. com. Juan Diego Pacheco & Andrés Beita, 2016. 7. Pers. com. Helena Molina, 2016. 8. Unpublished data JSV & JC. 9. Juan Esteban Barquero In Prep. 10. Seen again in 2012 by JC. * = only some isolated shoots in the last 15 yrs., pers. obs. JC.

RGM. Seagrasses on the Caribbean coast have been found up to 8 m deep. The most studied location and with the highest number of species reported for the Caribbean coast is PNC, with four species of seagrass and a total of 37 herbarium samples, dating back to 1975. The oldest samples of seagrasses found were *Thalassia testudinum* at Puerto Limón from 1963 and of *Ruppia maritima* at Moín from 1965 (Table 1). Seagrass area for the Caribbean coast is estimated as 360 400 m^2 (36.0 ha).

Seagrasses have been found at 21 locations on the Pacific coast, 13 of them reported here for the first time (Table 2). On the Pacific coast

of Costa Rica, the locations with seagrasses consist mainly of sheltered bays in the northern Pacific coast (eight locations), central Pacific coast (four locations), and the southern Pacific coast (nine locations) (Fig. 1). The most extensive meadow currently present in the Pacific coast is located at Playa Colibrí in Golfo Dulce, with an area up to 900 000 m^2 and three seagrass species (Table 2). At Bahía Culebra, only isolated shoots of *R. maritima* have been sighted in the last ten years. Seagrasses on the Pacific coast have been found up to 8 m deep. The oldest herbarium samples refer to *R. maritima* collected in 1967 from Playas del Coco (Table 2). Seagrass area for the Pacific coast is estimated as 967 984 m^2 (96.8 ha).

A total of 43 studies were found that included or reported seagrasses in Costa Rica, and the number of studies has been steadily increasing over time (Fig. 2). The majority of the studies were done in meadows along the Caribbean coast, and publications on seagrasses from the Pacific coast only appeared after the year 2000 (Fig. 2). Most studies have been taxonomic reports, followed by some ecological studies and monitoring, with recent focus on associated fauna (Fig. 3). The top three most studied species are *T. testudinum*, followed by *Syringodium filiforme* and *H. baillonis*, and the least studied species is *H. beaudettei* (Fig. 3).

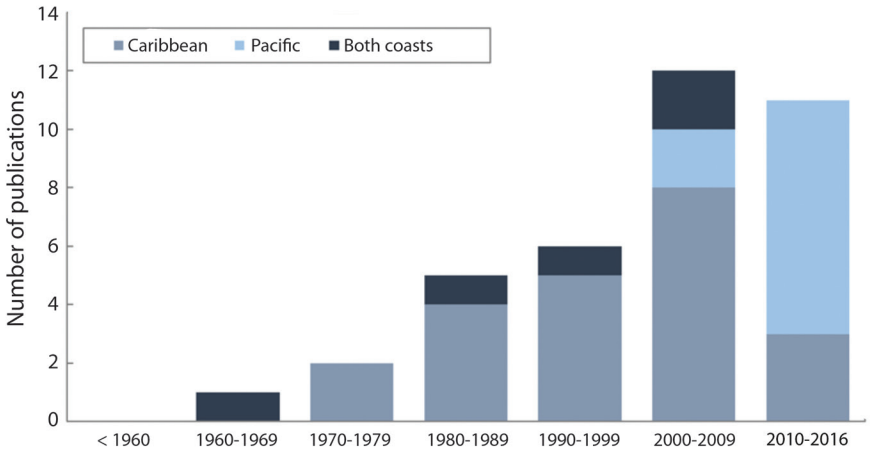

Fig. 2. Number of publications on Costa Rican seagrasses per coast by time period up to December 2016.

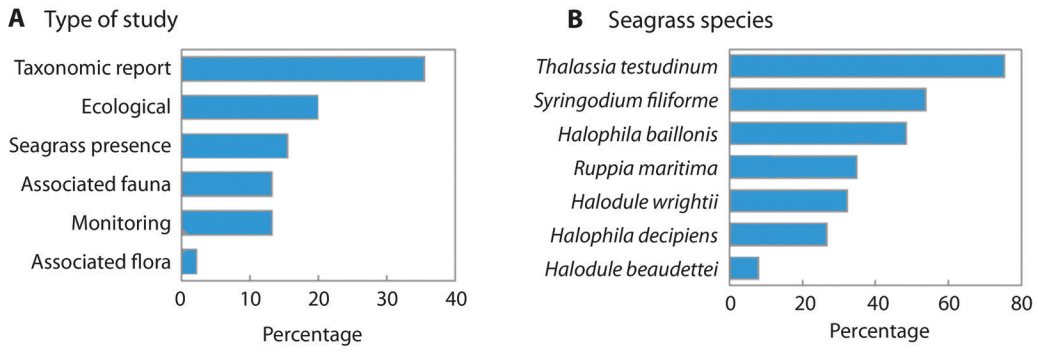

Fig. 3. Percentage of studies on seagrasses of Costa Rica up to December 2016 by (**A**) type of study, n = 43; and (**B**) species, n = 37 (percentage indicates the number of the total publications in which that species was mentioned).

DISCUSSION

Seven seagrass species have been reported for Costa Rica; however, a number of taxonomic considerations have to be taken into account. Two key aspects are potential misidentifications of seagrass species and the taxonomic standing of some species (Short et al., 2011). The current species name of the clover grass is *H. baillonis*, though there is discrepancy among specialists whether *Halophila baillonii* should be the correct species used (see Kuo & Wilson, 2008 for a detailed discussion on the taxonomic standing of the clover grass). In the past, the species *H. baillonis* has been misidentified with *Halophila decipiens* (Kuo & Wilson, 2008). The only record of *H. baillonis* in the Caribbean of Costa Rica was by Dawson (1962), which may have been *H. decipiens*, illustrations were not included. In contrast, *H. decipiens* has been correctly reported for the Caribbean of Costa Rica, with many herbarium samples, and it is currently present at Isla Uvita. Nonetheless, *H. baillonis* has recently been reported in the Caribbean Sea at Belize (Short, Fernandez, Vernon, & Gaeckle, 2006), Honduras (Caviedes-Sánchez & Carrasco, 2016), and in the Atlantic coast of Brazil (Barros, Costa, & Rocha-Barreira, 2014; Magalhães, Borges, & Pitanga, 2015); thus, the record by Dawson (1962) may have been correct, and it is also possible that this inconspicuous species may still be found along the Caribbean coasts of Costa Rica.

Another case of misidentification was *Halophila engelmannii*, reported for the Pacific coast of Costa Rica from a single specimen at the herbarium of the Universidad Nacional Autónoma de México (UNAM) (MEXU-1249952) (Crow, 2003b). High definition photographic material for this specimen was carefully studied by us and we consider the correct species to be *H. baillonis*. The specimen has four short leaves per foliar shoot with oval apices and defined petioles, similar to *H. baillonis* (Kuo & Den Hartog, 2001; Van Tussenbroek, Santos, Wong, Van Dijk, & Waycott, 2010). In addition, *H. engelmanni* has not been reported along the Pacific coast elsewhere (Phillips & Menez, 1988; Green & Short, 2003).

The taxonomy of *Halodule* needs to be clarified. *H. beaudettei* is considered by some to be a synonym of *Halodule wrightii*, as it has been argued that leaf-tip morphology is insufficient to define the taxonomic status of the species within this genus (Phillips, 1967). The specimens of *H. beaudettei*, reported here for the first time for the Pacific coast, present an acute median tooth differing from samples of *H. wrightii* from the Caribbean coast (Kuo & Den Hartog, 2001; Van Tussenbroek et al., 2010). Genetic analyses on *H. wrightii* from the Caribbean and *H. beaudettei* from the Pacific of Costa Rica are currently under way.

Ruppia maritima has been reported for both coasts; however, its verified current presence is extremely limited. In the Caribbean, there is only one herbarium sample from 1965 supporting its presence but there have been no other sightings of this species. On the Pacific coast, there are multiple herbarium samples of this species; yet the only reported meadow disappeared in the mid-1990s; with only some isolated shoots noted in the northern and central Pacific coast in the last 15 years (pers. obs. JCN & pers. com. Eleazar Ruiz). In Mexico, specimen of this species previously identified as *R. maritima* were considered to belong to a new species *Ruppia mexicana* (Den Hartog, Van Tussenbroek, Wong, Mercado-Ruaro, & Márquez-Guzmán, 2016), and therefore careful examination of specimens from Costa Rica should clarify their taxonomic status. A final cautionary note on species in Costa Rica: the newly introduced *Halophila stipulacea* in the Caribbean has not been found in Costa Rica. Considering its rapid expansion throughout the Caribbean (Willette et al., 2014; Van Tussenbroek et al., 2016) it is most likely just a matter of time before this species will be found on the Caribbean coast of Costa Rica.

Different seagrass species occupy the Pacific and Caribbean coasts of Costa Rica with distinct habits in each coast. In the Eastern Tropical Pacific (ETP), seagrasses belong to the genera *Halophila*, *Halodule* and *Ruppia*

(Cortés, 2001; Green & Short, 2003; Short, Carruthers, Dennison, & Waycott, 2007). These seagrasses are mainly small pioneer or opportunistic species, which can also be ephemeral (Orth et al., 2006; Kendrick et al., 2012). In the Caribbean, seagrass meadows are mostly dominated by the large species *T. testudinum*, the faster growing *S. filiforme*, and opportunistic ephemeral *H. wrightii* (Orth et al., 2006; Van Tussenbroek et al., 2010; Kendrick et al., 2012). In the Pacific, seagrasses develop in deeper or more turbid waters than in the Caribbean, where they are found in shallow coastal or reef lagoons. Even so, both coasts of Costa Rica belong to the Tropical Atlantic seagrass bioregion (Short et al., 2007).

The number of seagrass locations is higher in the Pacific than the Caribbean; yet Caribbean locations are mostly large meadows (Cortés, Soto, & Jiménez, 1994; Cortés & Jiménez, 2003), while in the Pacific the largest meadow is found in the southern Pacific coast with many smaller patches. Seagrass presence in the Caribbean is restricted to a sheltered island habitat in the central coast and coral reef lagoons in the southern areas of the Caribbean coast (Cortés & Guzmán, 1985; Cortés, 2016b). The northern Caribbean coast of Costa Rica is rectilinear, has high wave energy and precipitation leading to higher river effluent than the southern Caribbean, likely hindering seagrass presence there (Cortés, 2016b). Given limited research, current estimates of seagrass coverage in Costa Rica are considered to be an underestimation of actual seagrass area.

On the Pacific coast of Costa Rica, following seagrass loss in the northern Pacific coast in the mid-1990s (Cortés, 2001), there were no other known extant seagrass meadows, until 2009 and 2010 when seagrasses were reported in the southern Pacific coast (Bessesen & Saborío-R., 2012; Samper-Villarreal, Bourg, Sibaja-Cordero, & Cortés, 2014; Sarmento de Carvalho, 2013; Sarmento, Chaves, Retamosa, Ruepert, Jiménez, & Blanco, 2016). In this area, seagrasses have been continuously sighted since, and here we report an additional five new locations. The new sightings may indicate recent colonization by seagrasses in this sheltered fjord-like estuary; however, residents recall the presence of seagrasses at some of these sites for decades.

Seagrass research in Costa Rica has been limited, but has been steadily increasing. Forty-three studies on seagrasses were found, most of which were either taxonomic reports or site descriptions. Presence of seagrasses has also been reported in studies on other organisms such as marine turtles (Sarmento de Carvalho, 2013; Chacón-Chaverri, Martínez-Cascante, Rojas, & Fonseca, 2015a, 2015b; Sarmento et al., 2016), corals (Fernández & Alvarado, 2004), and fish (Myers, Wagner, & Vaughan, 2011). Seagrasses in Costa Rica are subtidal, and are only exposed during the maximum low tides. The absence of large exposed intertidal seagrass beds which can be easily accessed at low tide, common in the Indo-Pacific or temperate regions (Moore & Short, 2007; Van Tussenbroek et al., 2007), may be an important reason for limited research effort on Pacific seagrasses. The search for seagrass populations in the Pacific is more challenging than in the Caribbean. Pacific seagrass species are smaller, more ephemeral, and occur in deeper or more turbid waters, with tidal ranges 3 m or higher (Lizano, 2006); while Caribbean meadow species are larger and grow in clearer and calmer waters, with a tidal range of 0.3-0.5 m (Cortés, 1998; Lizano, 2006). In the Caribbean, there has been one continuous monitoring program in place since 1999, the Caribbean Coastal Marine Productivity Program known as CARICOMP (Fonseca, Nielsen, & Cortés, 2007; Cortés et al., 2010); which accounts for all the monitoring publications focusing on plant biomass, productivity and turnover rates. Studies on grazing and non-charismatic organisms associated with seagrass meadows are very limited, with only one study focused on macroalgal epiphytes in the Caribbean (Samper-Villarreal, Bernecker, & Wehrtmann, 2008), and one study mentioning limited grazing and associated macrofauna in the southern Pacific (Samper-Villarreal et al., 2014). Seagrasses in the southern Pacific coast are known

as a resting, breeding and foraging area for green sea turtles and they are important locations along migratory routes (Bessesen & Saborío-R., 2012; Sarmento de Carvalho, 2013; Chacón-Chaverri et al., 2015a, 2015b). Given the Vulnerable status of *H. baillonis* according to the IUCN red list (Short et al., 2011) and the importance of these meadows for sea turtles, conservation and management initiatives of these meadows is warranted.

Seagrasses in Costa Rica are subjected to multiple disturbances, and further research on seagrass meadows in Costa Rica is urgently needed to establish management and conversation initiatives. Loss of seagrasses in the northern Pacific coast followed a severe storm resulting in light deprivation from increased and prolonged water turbidity, and uprooting of the plants (Cortés, 2001). These seagrass meadows have shown no signs of recovery to date. In 1991, the Limón Earthquake caused coastal uplifting of the Caribbean coast (Cortés, Soto, Jiménez, & Astorga, 1992; Cortés et al., 1994; Cortés & Jiménez, 2003), which resulted in the subaerial exposure and subsequent die-off of more than 40 000 m^2 of seagrass (Cortés et al., 1992; Cortés et al., 1994). Another impact was whitening and shedding of *T. testudinum* leaves in 2005 following heavy storms at Manzanillo; but leaf regrowth shortly resumed afterwards and no permanent damage to the meadows was reported (Krupp, 2006; Krupp et al., 2009). The long-term monitoring program in Caribbean meadows has revealed a decline over time, most likely due to increased turbidity (Van Tussenbroek et al., 2014). In November 2016 Level 4 hurricane Otto passed through the country, with high wave and wind energy and increased precipitation. Other threats are local, such as increased turbidity from land alteration, increased nutrient runoff, and anchoring on seagrass meadows (Cortés & Risk, 1985; Orth et al., 2006; Cortés et al., 2010). Further research, monitoring, management and conservation strategies are needed for Costa Rican seagrasses, with a stronger focus needed on research looking at associated fauna and flora, and incorporating ecosystem resilience and services.

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RESUMEN

Pastos marinos de Costa Rica: del majestuoso Caribe a las praderas dinámicas del Pacífico Este Tropical. Las praderas de pasto marino están deteriorándose a nivel mundial ligado a disturbios antropogénicos. Esta degradación resalta la necesidad de entender las dinámicas ecológicas de estos sistemas costeros para definir estrategias de manejo y conservación adecuadas. Aquí, nosotros analizamos el conocimiento actual sobre praderas de pastos marinos en las costas Caribe y Pacífico de Costa Rica, América Central. El conocimiento actual se basó en revisiones de literatura, colecciones de herbarios, entrevistas y observaciones personales. Reportamos un total de cinco géneros y siete especies para Costa Rica: *Thalassia testudinum*, *Syringodium filiforme*, *Halophila decipiens*, *Halophila baillonis*, *Halodule wrightii*, *Halodule beaudettei* y *Ruppia maritima*. Se reportan seis especies para el Caribe y cuatro especies para el Pacífico. *Thalassia testudinum*, *S. filiforme* y *H. decipiens* solamente han sido reportadas para el Caribe. *Halodule beaudettei* está solamente en la costa Pacífica. *Halophila baillonis*, *H. wrightii* y *R. maritima* son reportadas para ambas costas. Se encontraron pastos marinos en un total de 31 sitios en Costa Rica, la mayoría en el Pacífico; 16 de los cuales se reportan aquí por primera vez. Las praderas de pastos marinos de ambas costas son sumamente diferentes. En el Caribe, hay praderas extensas dominadas por una especie grande, *T. testudinum*, las cuales han estado presentes por décadas. En contraste, las praderas en la costa Pacífica son más dinámicas ya que están dominadas por especies pioneras y efímeras, principalmente *H. baillonis* y *H. beaudettei*. El número de estudios sobre pastos marinos en Costa Rica es limitado, pero ha estado

creciendo de manera constante, enfocándose principalmente en reportes taxonómicos y ecología de *T. testudinum* en la costa Caribe. Esfuerzos de investigación, conservación y de manejo se verían beneficiados por una continuación del monitoreo e investigación detallada en pastos marinos, pero también sobre la flora y fauna asociada, incorporando análisis de resiliencia del ecosistema y sus servicios.

Palabras Clave: Praderas de pasto marino, fanerógamas, humedales costeros, Pacífico Este Tropical, Caribe, América Central, Centroamérica, inventario.

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