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The Antillean manatee (*Trichechus manatus manatus*) along the Caribbean coast of Colombia: underused incidental records help identify present and past coastal-lowland hotspots

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The Antillean manatee (*Trichechus manatus manatus*; hereafter “manatee”) ranges from Mexico and the Bahamas south to Brazil and is listed as Endangered by the IUCN (Self-Sullivan & Mignucci-Giannoni, 2008). Castelblanco-Martínez et al. (2012) compiled expert estimates to suggest a total meta-population size of 6,700 animals for the Western Atlantic region. Apart from the manatees in the Colombian Orinoco and Amazon drainage basins, only about 400 manatees are believed to persist in the subpopulations inhabiting the Colombian-Caribbean drainage basin (Castelblanco-Martínez et al., 2012) and occur principally in the river systems of the Magdalena, Sinú, and Atrato rivers. Manatees fulfil a unique niche in this freshwater ecosystem due to their extensive consumption of aquatic plants. The species may be especially important in recycling scarce nutrients and maintaining waterway quality for navigation, flood control, mosquito control, and fish habitat (Allen & Keith, 2015; Allsopp, 1969; Duplaix & Reichart, 1978; Etheridge et al., 1985; National Science Research Council of Guyana & National Academy of Sciences, 1974; United Nations Environment Programme, 1995). Unfortunately, all these benefits remain poorly appreciated and the animals continue to be frequently killed for consumption (Quintana-Rizzo & Reynolds, 2010). Inside Colombia, the species has been studied significantly only in the Orinoco (Castelblanco-Martínez,

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Bermúdez-Romero, et al., 2005) and inland freshwater areas of high manatee density such as in the Ciénaga de Paredes of the upper Magdalena River basin (Arévalo-González et al., 2014; Castelblanco-Martínez, Holguín, et al., 2005). More recently, manatee occurrence has also been studied in the middle to upper reaches of the Atrato River (Caicedo-Herrera et al., 2014), the Ciénaga Grande de Santa Marta (Guerrero & Lugo, 2007) and in a 60 km lower section of the Magdalena River just before entering Barranquilla (Mahecha, 2013) (Figure 1). Most conservation, activity-pattern, and population-assessment research has focused on such areas of main population density. Very little is known about manatees in areas that are not designated as protected habitat or in areas of lower manatee densities, or seeming fringe or understudied habitat areas, which nevertheless are fundamental to understanding the ecology of this endangered species and its restoration (Hieb, et al., 2017; Pabody et al., 2009).

Identifying areas of key importance in the life history of endangered species is valuable because it can help prioritize conservation and awareness efforts. Besides several well-studied areas of high manatee population density in Colombia, little is known about the existence of other areas of potential importance to the species. Because manatees are a very wide-ranging species found in at least 45,000 km² of wetland habitats of the country (lakes, rivers, streams, flood plains, estuaries, and other seasonally flooded areas), Castelblanco-Martínez et al. (2015) have highlighted the challenges this presents to effective conservation. Therefore, identifying additional areas of special importance to manatees based on incidental and underused records of occurrence can help target conservation research and management efforts to these additional key sites and may make the combined conservation effort much more effective.

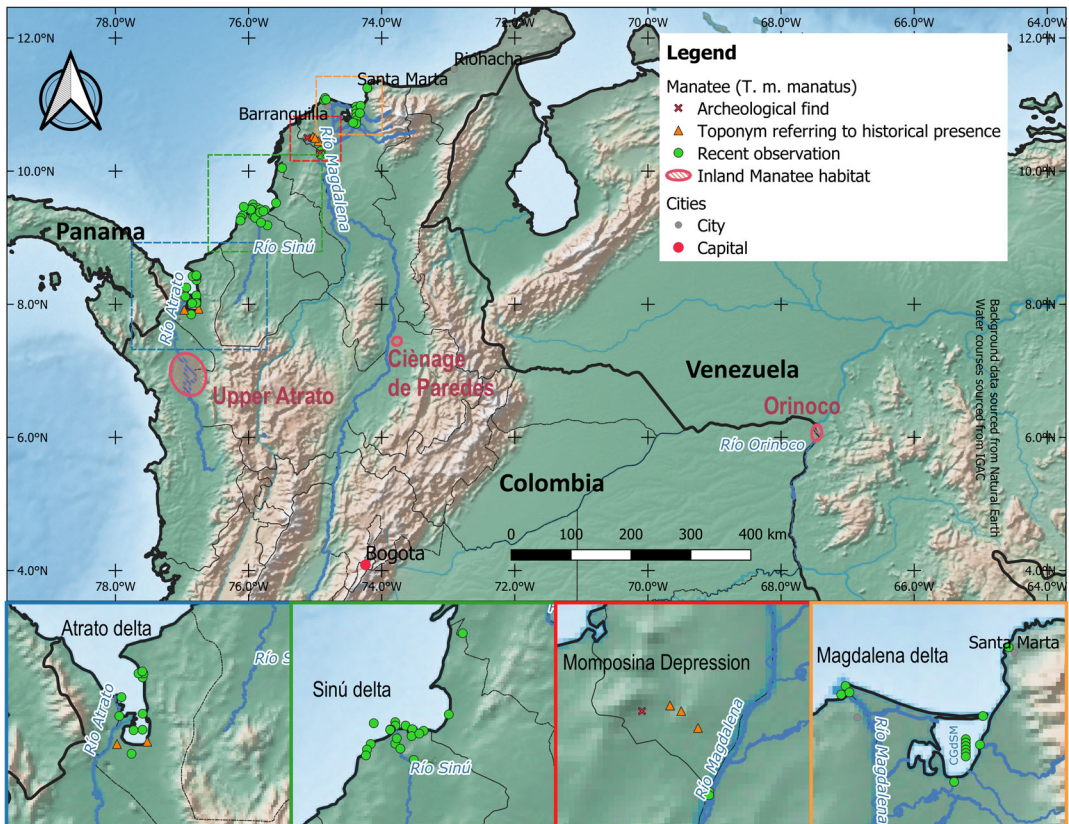


FIGURE 1 Map of 51 incidental coastal and coastal-lowland records of the Antillean manatee in Colombia, as documented in Table 1. Insets below from left to right showing the records for the Atrato and Sinú deltas, the Momposina Depression, and the Magdalena delta, respectively.

Manatees show a strong preference for freshwater but also frequent coastal estuarine and marine waters. Satizabal et al. (2012) provided evidence that genetic exchange between spatially isolated subpopulations of the West Indian manatee is mediated by highly dispersive males (Castelblanco-Martínez et al., 2012). Manatees in Colombia benefit from a relatively extensive and detailed protection plan, broadly supported by the public and many universities and nongovernmental parks and conservation organizations (as listed by Caicedo-Herrera et al., 2004). Even so, protected areas only constitute a small fraction of the total area of occurrence of the manatee. For example, Castelblanco-Martínez et al. (2015) showed that 89% of manatee habitat in the Colombian-Caribbean basin lies outside of protected areas and they stressed the importance of broader protection. Similarly, Satizabal et al. (2012) stressed the urgent need to extend protection from a purely riverine basis to a wider scale to help preserve genetic connectivity in this species. As the only way for manatees of different river systems to connect is via the sea, safe passage through estuarine and coastal marine waters is critical to maintaining their genetic integrity. This may become more critical if populations remain small or continue to decline.

The most extensive and most recently published review of manatee records for Colombia was conducted in 2001 and compiled 153 opportunistic manatee records spanning the period 1950–1995 and collected from a variety of sources (Montoya-Ospina et al., 2001). That review only documented 14 records of manatees for Caribbean coastal areas or rivers in the Caribbean region. Since then, aside from dedicated studies by Guerrero and Lugo (2007) and Mahecha (2013) in areas of high manatee density, Caicedo-Herrera et al. (2014) conducted the most recent dedicated survey of manatee distribution in the Atrato part of its range. In absence of current systematic studies, compiling opportunistic and incidental records is valuable because it can provide evidence of manatee dispersal activity, help to discern movement routes or be used to identify additional areas in need of special protection. For example, Kiszka (2014) interviewed 508 Colombian fishers in 28 villages of the Sinú and Magdalena river basins and found that 93% of the fishermen spoke of the presumed existence of coastal manatee hotspots even though their location was not or could not be indicated. Where information is lacking, the local and traditional knowledge of fishers is valuable in the study of rare or endangered fauna (e.g., Choi-Lima et al., 2017; Franzini et al., 2013). The identification of the potential coastal lowland manatee hotspots alluded to by fishers (Kiszka, 2014) and their effective inclusion into the protected areas network, could provide a much-needed boost to manatee conservation in Colombia. The findings of Satizabal et al. (2012) suggest that coastal manatee hotspot areas may play a pivotal role in maintaining genetic exchange between manatee subpopulations and should therefore be considered as high priority areas for conservation. For cryptic megafauna species (like the manatee) in which detailed and in-depth studies are difficult or remain lacking, the mapping of occurrences, sightings, and other types of records can be an initial step towards identifying areas of priority or special interest to conservation (e.g., Debrot et al., 2020), similar to other rare and endangered marine species (e.g., Leopold et al., 2019). Unfortunately, scattered incidental records of marine megafauna are typically not available to science. These often remain hidden in agency reports or informal sources, poorly documented, or not taken up into the literature and as a result are underused (Nazareth et al., 2022; Pikesley et al., 2012).

Colombia is roughly divided into five major biome regions (MADS & IDEAM, 2014), one of which is known as the “Colombian Caribbean region.” The Colombian Caribbean biome region is characterized by xerophytic and subxerophytic vegetation types that correspond to arid and semiarid lowland areas with meandering rivers (Sanchez-Cuervo et al., 2012). The objective of this study was to compile scattered opportunistic and incidental records of manatee occurrence in the Colombian Caribbean region to help identify or substantiate additional lowland, lower-river, and/or coastal areas of manatee priority. To this end, we searched Google and Google-Scholar using both Spanish and English keywords for online sources and accounts of manatees for all cities, coastal protected areas, and rivers of the Colombian Caribbean coast and up to 50 km inland. With one exception (United States Department of the Interior [USDI], 1965) the sources found were dated 2001–2019. As specific incidents were occasionally found documented in more than one unofficial source (e.g., both online newsletter and newspaper or multiple online newspapers), we had to guard against double counting by checking for overlap between dates, locations, and other details. Additionally, live-stranded animals that were subsequently released, were sometimes reported twice in the media or

management accounts (typically once upon stranding and once upon release). In such cases we chose the release location as the “site record” for mapping, as this also typically came with exact GPS coordinates. Park management reports and plans describing the general association of manatees with mangroves or other aquatic habitat but not stating outright that manatees could be confirmed for the area in question, were not counted as a manatee record. We also excluded sightings generated from two intensive, directed population studies conducted in lowland areas of manatee concentration (Guerrero & Lugo, 2007; Mahecha, 2013) as the nature of such records is completely different from that of incidental occurrence records. These two studies took place in areas that could (additionally) be identified as manatee hotspots based on our compilation of incidental records. Hence, we do cite these studies in our discussions of the areas in question.

In our review we compiled a total of 51 incidental manatee records, most of which were found in online published or relatively recent online-accessible gray literature sources, such as theses, institutional reports, and area management plans, but also in online newspapers. The records they provided largely spanned the 41-year period of 1978–2019. The archaeological records (i.e., pre-Hispanic and as old as 3300 BC) and persistent place names (toponyms), were much older. We identified the type of aquatic habitat for each record along the land-sea gradient as: (1) lower-river, riverine, stream, canal, or lake freshwater habitat; (2) estuarine river-mouth habitat; (3) mangrove lagoon habitat or (4) marine open coast habitat. A full chronological listing of the records for each of the four identified principal clusters is provided in Table 1. Table 2 gives a summary of various data that were extracted from the records (depending on the degree of documentation that could be found). Twenty of the records were previously incorporated into formal manatee studies or reports: $n = 14$ records, Montoya-Ospina et al. (2001); $n = 3$ records, Moreno-Bejarano and Álvarez-León (2003); $n = 3$ records, Omacha and Corpourabá (2016). We identified, 31 new (and difficult to find) records, including them in a formal manatee study for the first time and making them available for broader biogeographic assessments of manatees. We distinguished six types of records in Table 1 as follows: (1) “stranding” records were for animals washed up on shore either dead or alive and whether due to entanglement in fishing gear. In the case of live stranding, the animal was often rescued and returned, and often also reliably GPS-tagged and tracked. (2) “tracking” record locations came from the first GPS position recorded on a tagged manatee. However, if a rescued animal died and was not returned alive, it was listed as a “stranding” record. (3) “toponym” records were persistent place names with the word manatee. When toponyms are based on animal names, they are taken to suggest the species' former presence at the specific location. With toponyms there is a real possibility that they were derived erroneously, based on incorrect or unsubstantiated sightings, or were named for other reasons. While not proof of a species' former presence, they are still considered valuable because they can provide clues about the historical biogeography of rare species (Adam & Garcia, 2003). (4) “Capture” records refer to all records in which animals were either caught passively in fishing gear or actively hunted and killed. (5) “Sighting” records were reported by local fishers, nature managers, scientists, or dive operators. In most cases no photographic material was available for independent verification, and we fully relied on the local expertise of the observers in being able to distinguish manatees from other sympatric megafauna such as dolphins (e.g., *Sotalia fluviatilis*), crocodylians (*Caimanus crocodilus*, *Crocodylus acutus*), and the capybara (*Hydrochoerus hydrochaeris*). (6) “Archaeological” records originated in archaeological excavations of pre-Hispanic human sites of habitation.

Of the 51 records presented, 14 represent incidences of fisheries bycatch or hunting and slaughter, 7 of stranding, 23 of sightings and/or animals released for tracking, 5 were toponyms, and 2 were archaeological records (Table 2). Excluding ancient archaeological records, the habitats associated with the records presented were as follows: 18 from marine open coasts, 10 each from mangrove lagoons, and estuarine river mouths, and 11 from assorted freshwater habitats (Table 2). The records from Table 1 were mapped in Figure 1 whereby toponyms and archaeological finds were individually mapped, and all other records were mapped as “recent observations” (Figure 1).

The most salient results show that lower-river and coastal manatee records were principally documented in three coastal clusters (Figure 1). These are all located in or in the vicinity of the deltas of three river systems known to harbor the main surviving manatee populations, primarily in the mid- to upper-stream reaches. From east to west

TABLE 1 Overview of supporting information on 51 manatee records for the Colombian Caribbean coast and coastal lowlands as discussed in the text and mapped in Figure 1.

River or system/ Record no.	Location	Date	Habitat	Type of record	Latitude °N	Longitude °W	Published manatee source	Further documentation	Number per sex	Comment
Magdalena										
1	Río Fundación-Caño Palenque (CGdSM)	1978	Freshwater river	Sighting	10.72809	74.42850	Moreno-Bejarano & Álvarez-León (2003)		U	
2	CGdSM	1985	Mangrove lagoon	Capture	10.86667	74.38333	Montoya-Ospina et al. (2001)		U	Killed
3	Dársena del Tajamar oriental de Río Magdalena (1989)	1989	Estuarine river mouth	Sighting	11.07536	74.83481	Moreno-Bejarano & Álvarez-León (2003)		U	
4	CGdSM	1992	Mangrove lagoon	Capture	10.86667	74.38333	Montoya-Ospina et al. (2001)		F	Later died
5	CGdSM	1995	Mangrove lagoon	Capture	10.86667	74.38333	Montoya-Ospina et al. (2001)		2U	One killed one later died
6	CGdSM	1997	Mangrove lagoon	Capture	10.86667	74.38333	Montoya-Ospina et al. (2001)		U	Killed
7	Barranquilla	pre- 2001	Marine open coast	Sighting	11.06667	74.86667	Montoya-Ospina et al. (2001)		U	
8	Desembocadura de los ríos Frio-Sevilla (CGdSM)	2003	Mangrove lagoon	Sighting	10.87224	74.32810	Moreno-Bejarano & Álvarez-León (2003)		U	
9	CGdSM	May 2004	Mangrove lagoon	Capture	10.98333	74.31667	This paper	Herrera (2004)	M	Saved from fishermen
10	CGdSM	June 2015	Mangrove lagoon	Stranding	10.86667	74.38333	This paper	Seguimiento (2015)	M	Cause: fish kill
11	El Morro	Jan 2017	Marine open coast	Sighting	11.25000	74.21667	This paper	García (2017)	U	
12	Bocas de Cenizo	Mar 2017	Estuarine river mouth	Capture	11.10000	74.85000	This paper	https://www.klenyke.com/noticias/especies-de-manatiles-en-columbia	U	Killed
13	CGdSM	Feb 2019	Mangrove lagoon	Stranding	10.86667	74.38333	This paper	https://www.publimetro.co/co/colombia/2019/02/16/muere-ultimo-manati-macho-habia-cienaga-grande.html	M	Dead

(Continues)

TABLE 1 (Continued)

River or system/ Record no.	Location	Date	Habitat	Type of record	Latitude °N	Longitude °W	Published manatee source	Further documentation	Number per sex	Comment
Momposina Depression										
14	Puerto Chacho, Canal del Dique, Arjona	prehistoric	NA	Archeological find	10.10000	75.40000	This paper	Álvarez-León & Maldonado-Pachón (2010)	2U	
15	Basurero de Monte Sión, Repelón	prehistoric	NA	Archeological find	10.50000	75.11667	This paper	Álvarez-León & Maldonado-Pachón (2010)	U	
16	Ciénaga Manatí	historic	Freshwater lake	Toponym	10.51667	75.03333	This paper	US. Dept. Interior (1965)	NA	
17	Manatí municipality	historic	Freshwater	Toponym	10.50000	75.00000	This paper	US. Dept. Interior (1965)	NA	
18	Manatí town	historic	Freshwater river	Toponym	10.45000	74.95000	This paper	US. Dept. Interior (1965)	NA	
19	Calamar	1990	Freshwater canal	Capture	10.25000	74.91667	Montoya-Ospina et al. (2001)		M, F, 5U	Three killed, three captured alive, one released
20	Calamar	1991	Freshwater canal	Capture	10.25000	74.91667	Montoya-Ospina et al. (2001)		3M, 2F, 5U	Four killed, five released, one unintentional death
Sinú										
21	Sinú river mouth	1989	Estuarine river mouth	Capture	9.45000	75.93333	Montoya-Ospina et al. (2001)		U	Died in captivity
22	Sinú river mouth	1991	Estuarine river mouth	Capture	9.45000	75.86667	Montoya-Ospina et al. (2001)		M, F	Both later died
23	Sinú river mouth	1995	Estuarine river mouth	Capture	9.33333	75.93333	Montoya-Ospina et al. (2001)		U	Killed
24	Sinú river mouth	1995	Estuarine river mouth	Capture	9.45000	75.93333	Montoya-Ospina et al. (2001)		3U	All killed
25	Ciénaga grande, Lorica	pre-2001	Freshwater lagoon	Sighting	9.18600	75.71600	Montoya-Ospina et al. (2001)		U	
26	San Bernardo del Viento	2003–2014?	Marine open coast	Sighting	9.36766	75.92339	This paper	Fundación Omacha y CVS	U	
27	San Bernardo del Viento	2003–2014?	Marine open coast	Sighting	9.30069	75.90042	This paper	Fundación Omacha y CVS	U	

TABLE 1 (Continued)

River or system/ Record no.	Location	Date	Habitat	Type of record	Latitude °N	Longitude °W	Published manatee source	Further documentation	Number per sex	Comment
28	Delta Sinú	2009	Estuarine river mouth	Tracking	9.42534	75.96121	This paper	Fundación Omacha y CVS	M	Released and named Mac Giver
29	Moñitos	2009	Marine open coast	Sighting	9.25739	76.12298	Omacha & Corpouraba (2016)		U	
30	Paso nuevo	2009	Marine open coast	Sighting	9.33107	76.09256	Omacha & Corpouraba (2016)		U	
31	Delta Sinú	2011	Estuarine river mouth	Tracking	9.42579	75.96529	This paper	Fundación Omacha y CVS	F	Released and named Julieta
32	Moñitos	2011	Marine open coast	Tracking	9.29521	76.11625	This paper	Fundación Omacha y CVS	M	Released and named Romeo
33	Delta Sinú	2012	Estuarine river mouth	Tracking	9.42284	75.96657	This paper	Fundación Omacha y CVS	F	Released and named Ruby
34	Punta Los Mestizos	2015	Marine open coast	Sighting	9.46521	76.07244	This paper	Fundación Omacha y CVS	F	Released and named Margarita
35	Caño Saliado	2016	Estuarine river mouth	Sighting	9.38183	75.82778	This paper	Fundación Omacha y CVS, 2017	U	
36	El Roto	2016	Marine open coast	Sighting	9.25739	76.12288	This paper		U	Reported by fisherman
37	Santuario El Corchal Mono Hermandes	2016	Mangrove lagoon	Stranding	10.04711	75.49703	This paper	Report Parques Nacionales Naturales	U	Dead.
38	Tolú	Nov 2018	Marine open coast	Stranding	9.52242	75.58716	This paper	Fundación Omacha y CVS	M	Released and named Santiago
39	Caño Remedía pobre	2019	Freshwater river	Stranding	9.22775	75.81356	This paper	Fundación Omacha y CVS	U	Dead
Atrato										
40	Ciénaga de Manatí	historic	Freshwater lake	Toponym	7.60000	76.83333	This paper	US. Dept. Interior (1965)	NA	
41	Río Manatí, Brazo Manatí, Cano de Manatí ^a	historic	Fresh water stream	Toponym	7.93333	76.75000	This paper	Caicedo-Herrera et al. (2005); US. Dept. Interior (1965)	NA	

(Continues)

TABLE 1 (Continued)

River or system/ Record no.	Location	Date	Habitat	Type of record	Latitude °N	Longitude °W	Published manatee source	Further documentation	Number per sex	Comment
42	Necocil	1996	Marine open coast	Sighting	8.41667	76.78333	Montoya-Ospina et al. (2001)		U	
43	Golfo de Urabá	1996	Marine open coast	Capture	8.13333	76.78333	Montoya-Ospina et al. (2001)		U	Killed
44	Ciénaga Mariagua	2011	Mangrove lagoon	Capture	8.11667	76.95000	This paper	Cocomaquia Codechocó & WWF Colombia (2014)	U	Killed
45	Necocil	2015	Marine open coast	Sighting	8.42088	76.77749	Omacha & Corpouraba 2016		U	
46	Necocil	2016	Marine open coast	Stranding	8.42088	76.78821	This paper	Fundación Omacha y Corpourabá	U	
47	Bocas del Atrato	2017	Marine open coast	Sighting	8.01918	76.78431	This paper	Fundación Omacha y Corpourabá	U	
48	Bocas del Atrato	2019	Marine open coast	Sighting	8.25161	76.93446	This paper	Omacha y Corpourabá	U	
49	Necocil	2019	Marine open coast	Stranding	8.43506	76.78543	This paper	Omacha y Corpourabá	U	Dead
50	Puerto Antioquia	2019	Marine open coast	Sighting	8.01553	76.84828	This paper	Omacha y Corpourabá	U	
51	Puerto Antioquia	2019	Freshwater river	Sighting	7.84744	76.86269	This paper	Omacha y Corpourabá	U	

Note: The column "Published manatee source" indicates the first mention in the manatee scientific literature. "Further documentation" refers to supporting information such as agency reports, websites, or nonmanatee-related literature sources. Latitude and longitude reported as decimal degrees. CcdSM: Ciénaga Grande de Santa Marta; NA: not available; CVS: Corporación autónoma regional de los Valles del Sinú y del San Jorge; F: female; M: male; U: unknown sex.

*Same location known by three different names.

TABLE 2 Overview of key data characteristics for 51 incidental manatee (*Trichechus m. manatus*) records compiled for the Colombian Caribbean biome zone.

Characteristic	Magdalena delta	Momposina Depression	Sinú delta	Atrato delta	All areas combined
Habitat type					
Freshwater	1	7	2	3	11
Estuarine	2	NA	8	—	10
Mangrove lagoon	8	NA	1	1	10
Marine coast	2	NA	8	8	18
Type of record					
Sighting	5	—	8	6	19
Stranding	2	—	3	2	7
Tracking	—	—	4	—	4
Capture	6	2	4	2	14
Archaeological	—	2	—	—	2
Toponym	—	3	—	2	5
Group size (n)					
1	12	—	17	10	39
2	1	—	1	—	2
3	—	—	1	—	1
7	—	1	—	—	1
10	—	1	—	—	1
Sex					
M	3	4	4	—	11
F	1	3	4	—	8
U	10	10	14	9	43
Previously published	8	2	7	3	20
This study	5	5	12	9	31

Note: Columns show the number of records reported for each listed characteristic in each the four regional clusters identified and for all cluster areas combined. Abbreviations: NA = not applicable; F = female; M = male; U = sex unidentified. Archaeological records ($n = 2$) were excluded from the overview of habitat types, group size and sex. The latter two types of data characteristic were also not applicable to toponym records.

these include the Magdalena River (including the Ciénaga Grande de Santa Marta) the Sinú River and Atrato River (Montoya-Ospina et al., 2001). These findings are evidence of coastal manatee hotspots such as those alluded to by Kiszka based on traditional knowledge (2014). The largest numbers of records more recent than 2010, came from the Sinú (nine) and Atrato (eight) cluster areas and the fewest (three) from the Magdalena cluster area (Table 1). The persistent lack of records for the roughly 350 km northeastern coast of the country bordering Venezuela is also notable (Figure 1). Montoya-Ospina et al. (2001) previously described the paucity of manatee records for this sector of the Colombian coast and ascribed it to the lack of suitable habitat which could be functioning as a natural barrier to dispersal. Even so, there is high importance in being able to traverse that area in view of connectivity with the Venezuelan subpopulations and the rest of the Caribbean (Debrot et al., 2020).

If, as according to Satizabal et al. (2012), genetic exchange between subpopulations is strongly mediated by highly dispersive males, a divergent sex ratio might be expected for the animals in the coastal manatee hotspots. Excluding archaeological and toponym records, in the current sample of 63 manatees tallied from “recent” records, the sex of 19 animals (30%) was identified: 8 females and 11 males (Table 2). This sample was too small to enable conclusions regarding differences in sex ratios. However, both males and females were common, suggesting that these areas represent normal habitat for all manatees, not specifically males. Apparent group sizes were 39 cases of solitary individuals and five groups of 2, 2, 3, 7, and 10 individuals, respectively (Table 2).

In addition to these three coastal clusters, a fourth cluster was identified (about 50 km) inland from the coast based on two relatively recent published (capture) records, three toponyms, and two archaeological records (Table 1, records 14–20 and Figure 1). This suggests that both historically and prehistorically, the many large and often-interconnected lakes in the area in question, part of the Momposina Depression (MD) and through which the Magdalena River flows, were once a key manatee area.

We compiled a total of 13 manatee records for the Magdalena River delta area, only three of which were more recent than 2010. The area includes the Ciénaga Grande de Santa Marta (CGdSM) which accounted for 10 records (77%) and the port area of Santa Marta for three (23%). The port lies in Santa Marta Bay with an approximate area of 5 km² and an average depth of 20 m. Even though it is semiprotected as a bay, its open shape makes it subject to marine waves and swell and unsuitable to mangrove growth. The deep sandy bay is flanked by steep rocky cliffs and the port area is principally coral reef and seagrass habitats (Castro-Sanguino, 2003). The small Manzaneros River is the main patch of remaining manatee habitat in the port area but is highly urbanized and polluted. It has not been recognized as important to manatees (Montoya-Ospina et al., 2001) and most manatee records in the port area are probably of transient animals. The CGdSM forms part of the exterior delta of the Magdalena River, the largest river of Colombia, which on average discharges water at a rate of 7,000 m³/s (Twilley et al., 1999). The CGdSM covers a combined area of lagoons, creeks, and mangroves swamps of 1,280 km² and has long been designated as a protected area (Sanctuario de Flora i Fauna CGdSM and Vía Parke Isla de Salamanca; Castelblanco-Martínez et al., 2015). Notwithstanding its protected status, it is continuing in ecological decline due to pollution, sedimentation, freshwater diversion for agriculture and salinification (Elster et al., 1999; González, 1991; Perdomo et al., 1999; Röderstein et al., 2014). The predominant habitat in which manatees were reported in this cluster of records was the mangrove lagoon habitat and this cluster also had the highest relative frequency of (intentional) capture records of all areas studied (Table 2).

Our search yielded a total of 19 manatee records for the lower Sinú basin and delta area, nine of which were more recent than 2010. The Sinú River begins at 3,400 m above sea level and runs for approximately 350 km to the north, through largely uninhabited areas, ending at Boca de Tinajones in the Caribbean Sea. The central part of the basin is subject to agricultural runoff, while the lower basin has a higher level of habitation, which brings higher levels of contamination due to agricultural runoff and discards (Acosta, 2013). In 1938, the Sinú River underwent an important course change in its lower section, which gave way to the formation of a new delta at Boca de Tinajones, located near the Gulf of Morrosquillo, and the consequent abandonment of the old delta in the Cispatá Bay (Robertson & Chaparro, 1998). The river's use is regulated by a management plan and part of the lower Sinú, with its sparsely populated swamplands and well-forested sluggish streams, has been included in the Distrito de Manejo Integrado (DMI) Complejo Cenagoso del Bajo Sinú (Castelblanco-Martínez et al., 2015). Ramirez (2016) studied coastal and marine protected areas inside the Gulf of Morrosquillo and emphasized the importance of partnering broadly with local communities to foster their meaningful participation in protected area planning, management, and governance.

For the lower Atrato basin and delta area, our search yielded 12 records, eight of which are more recent than 2010 and two of which are longstanding toponyms (USDI, 1965). These allude to the historical importance of manatees in this area. The Atrato River dominates the freshwater contributions to the Gulf of Urabá system, forming an estuarine front (Restrepo & Kjerfve, 2004; Vélez Agudelo & Aguirre Ramirez, 2016). In the delta mangroves occupy about 6,513 ha (Thomas et al., 2007). The river influences the entire northeastern sector of the gulf with its

freshwater, expanding the surface area of highly suitable fresh to brackish-water manatee habitat far into the shallow sea. Not surprisingly, this was the cluster where marine open coast manatee sightings were most frequent (Table 2). Mejia-Fernandez (1991) refers to early colonial sources (Simón "Noticias Historiales," cited in West, 1957) that speak of an annual harvest in 1620 in the order of 30,000 manatees per year from the lower Atrato basin. By any standards today, this value sounds neither credible nor sustainable for any significant period. However, the same source also speaks of large herds of peccaries (Tayassuidae) that the lowland natives traded with the neighboring upland provinces and lends credence to the assertion that large numbers of manatees were being harvested from the surrounding areas. However, as manatee products were evidently being traded at that time, we suggest that the uncertain but clearly large number of manatees involved may have come from a wider area than only the Atrato basin. During an exploratory expedition in 1870, Selfridge (1874) reported that manatees were frequently caught in the Atrato River and its tributary Cacarica, from which he obtained a number of skulls. Based on these historical sources and our own compilation of records for the Atrato lower basin and delta in the Gulf of Urabá, we find evidence of the continuing importance of these areas as manatee habitat. Earlier, Fariás-Curtidor (2008) documented more than 30 indirect records of manatee presence (feces and signs of foraging) and one sighting for the delta, allowing it to be confirmed as habitat for the species. The importance of the lower Atrato and its delta have already been officially recognized as important for biodiversity and large parts of the area have recently been designated as an UNESCO World Heritage site of protected habitat in the Parque Nacional Natural Los Katíos (UNESCO, 2015). The municipality of Quibdó developed an integral ecological management plan for the whole Atrato basin (Braham & Mena-García, 2014). The Gulf of Urabá is an economically depressed region where its strategic position for drugs and arms trafficking, combined with the absence of law enforcement, has made forced displacement and extreme violence commonplace in this most insecure part of Colombia (Gómez Aguirre & Turbay, 2016). Manatee consumption is common and appears to be a combination of local traditions and opportunism. Hence, working together with local communities and fishermen is a critical basis for all progress (Omacha & Corpourabá, 2016).

In addition, to the three coastal cluster areas with recent manatee records, a more-inland cluster of toponyms and archaeological finds associated with the Momposina Depression (MD) (records #14–18, Table 1) suggest evidence of a lower-river, lacustrine manatee area of historical and prehistorical importance 50 km and more, upstream from the mouth of the Magdalena River. At the MD, the Magdalena River splits into two branches that eventually merge back into each other further downstream. This suggests that at one time in the past, the many large, often interconnected freshwater lakes in and around the MD, may have been important manatee habitat. One of these lakes, namely Ciénaga Machado, was identified as a recent manatee-area by Caicedo-Herrera et al. (2004). In addition, Montoya-Ospina et al. (2001) further mentioned 10 capture incidents from the two separated Magdalena River branches that course through the MD, while Mahecha (2013) more recently documented 20 recent records for an adjacent 60 km section of the Magdalena River. The lower stretches of the Magdalena River clearly still have a significant density of manatees and are deserving of much greater conservation attention than currently given. If the surrounding lakes of the MD are also still connected to the Magdalena river, this lacustrine region might still be active manatee habitat and of conservation importance or potential.

Based on a compilation of opportunistic and incidental sightings and records, we present new evidence to identify and substantiate additional areas of apparent lasting importance to manatees. Our compiled records clustered in areas near the coastal deltas of the three main rivers of Colombia (the Magdalena, Sinú, and Atrato rivers) and point to these as likely nodes of importance for manatee migration and genetic exchange. In addition, archaeological records and toponyms suggest a fourth more-inland, lower-Magdalena region of wetlands known as the Momposina Depression that may have been of importance to the manatee in the past, but which is of uncertain importance today. Detailed studies by others into habitat selection by manatees (e.g., Caicedo-Herrera et al., 2014; Mahecha, 2013), would suggest that the current distribution of manatees neither accurately reflects the historical distributional nor the innate distributional preference of manatees. For instance, Mahecha (2013) studied habitat distribution of manatees with access to a variety of habitats and found that the most important manatee areas were not straight sections of the river but areas with incipient oxbow lakes and levees where water flow was reduced,

allowing shallow-sloping banks and growth of preferred food species. Caicedo-Herrera et al. (2014) studied habitat distribution of manatees in the Atrato and found most signs of manatee presence in lagoons, followed by rivers, confluences, and streams, in that order. Their results along with the findings of de Oliveira Alves et al. (2013) for the Amazon (and other studies they cite), suggest that ideal manatee habitat will generally be in the lower reaches of the rivers and show a positive association with mangrove estuaries. Therefore, we hypothesize that in the past the main distribution of manatees must have been centered in the lower river sections and deltaic areas, a few of which we have been able to identify. We conclude that the current distribution of manatees is likely highly negatively influenced by higher human population densities, hunting pressure, habitat destruction, and disturbance in the coastal lowlands. This may be the reason why the species is currently largely concentrated in small clusters of habitat in less-populated areas upstream and inland (Figure 1).

A brief note on toponyms is in order. There are six officially recognized toponyms that refer to manatees in Colombia (USDI, 1965). One of these named Isla Manatí is situated in the Meta tributary of the Orinoco and was not pertinent to this paper. Three toponyms are clustered near the MD while two were located in the Atrato delta area. The number of toponyms found for the Colombian Caribbean is considerably more than were found for neighboring Venezuela where in turn more archaeological records were found (Debrot et al., 2020). Both are indications of presumed former importance of manatees, but quantitative comparisons based on such small numbers remains tenuous at best. There are likely more unofficial toponyms at local level (e.g., Punta Manatí, Venezuela; Debrot et al., 2020) but these are hard to find, sometimes difficult to recognize when based on a native language and may eventually be lost if they are no longer used or have been removed from maps (e.g., the toponym Manparía Cutu, Bonaire; Debrot et al., 2006). Even so, the toponyms we identified for Colombia clearly cluster with other manatee record types and prove their utility in studies of the historical biogeography of rare species (Adam & Garcia, 2003).

As in many countries (Joppa & Pfaff, 2009), the designation of protected areas in Colombia has been biased towards remote montane, coastal, or jungle areas (Forero-Medina & Joppa, 2010). Due to this bias, the Colombian Caribbean today ranks among the most endangered biome regions of the country (Forero-Medina & Joppa, 2010). Only 0.5% of its surface area falls within national or regional protected areas (Forero-Medina & Joppa, 2010) and, especially based on the findings by Montoya-Ospina et al. (2001) and Mahecha (2013), the value of more protected wetland and riparian habitat around the MD in this designated biome should be evaluated for manatee conservation.

Our findings suggest several important avenues for awareness, conservation, and research efforts that can be of use when updating Colombia's national manatee conservation and management plan (Caicedo-Herrera et al., 2004). Colombia's national manatee plan stresses the importance of community involvement in manatee monitoring and conservation. However, under conditions of poverty and without other viable sustainable local livelihood options, poor coastal communities will retain unsustainable traditional practices such as killing manatees (e.g., Adeel & Safriel, 2008; Debrot, Veldhuizen, et al., 2020). Therefore, to help build local support for manatee conservation, we recommend the development of ecotourism livelihood-options for the fishermen that could also incorporate manatee-related activities.

The large number of marine open coastal records we report in the vicinity of the Atrato and Sinú deltas show that in these relatively undeveloped parts of the Colombian coast, manatees still frequently venture out of their preferred fresh and brackish water habitat into saline habitats. Hence, key research questions to address include: (1) in which life-cycle phase are animals venturing out into the sea, (2) in what way are they making use of the coastal zone, (3) how dependent are they on the nearby presence of fresh or brackish water sources, and (4) how far are they moving or migrating? Finally, while this work illustrates the potential value of compiling incidental manatee records, it also demonstrates that key information (dates, sex, biometrics, cause of death, etc.) is often imprecise or even lacking (Tables 1 and 2). The national manatee plan also calls for a national stranding network for Colombia (Caicedo-Herrera et al., 2004). We also consider implementation of such a network a top priority as it could help enable more swift and effective manatee interventions and better and more-complete data collection. It could also serve as an effective platform for more broadly engaging the public.

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AUTHOR CONTRIBUTIONS

Adolphe Debrot: Conceptualization; data curation; funding acquisition; investigation; methodology; writing – original draft; writing – review and editing. **Dalila Caicedo-Herrera:** Validation; writing – original draft. **Isabel Gómez-Camelo:** Data curation; validation; writing – review and editing. **Camila Rosso:** Data curation; investigation; validation. **Jan Tjalling van der Wal:** Data curation; software; visualization. **Tony Mignucci:** Investigation; resources; validation; writing – review and editing.

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