



Searching for manatees in the dark waters of a transboundary river between Mexico and Belize: a predictive distribution model

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Abstract Antillean manatees in the Hondo River have been recorded from aerial and aquatic surveys, and interviews. However, these studies have been conducted only in the lower riverbed, leaving a gap of information about their presence and habitat characteristics in the rest of the river. We characterize and determine the ecohydrological variables influencing the presence and habitat use of manatees in the Hondo River. During 2017 and 2018, 30 based-boat field trips were conducted in five consecutive transects of 15 km each. A mixed methodology was used for manatee detection: side-scan sonar, direct sightings, and feces collection. Ecohydrological variables were measured in all transects and fixed points. The survey effort was

136.5 h. We recorded 123 manatees: 47% were observations during the boat-based surveys, 29% were at fixed points, and 24% were opportunistic. Additionally, 10 manatee feces were found. The first transect of the river showed the highest relative abundance for the two sampled seasons (windy = 0.27 manatees/km, dry = 0.55 manatees/km). According to the Poisson model, the estimated population was equal to 51 manatees. A random forest model suggested high probability of observing manatees in the first transects and decreasing at the upstream. The ecohydrological variables influencing the detection of manatees were conductivity, transparency, depth, and proximity to the Four Mile lagoon. The first two transects have ecohydrological characteristics that makes a benign environment for refuge, rest and feeding of manatees. We recommend carrying out conservation efforts in the first transects, such as protection and the regulation of boat transit.

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Introduction

The American manatee (*Trichechus manatus*) has two subspecies: The Florida manatee *T. m. latirostris* and

the Antillean manatee *T. m. manatus*, the latter listed on the IUCN Red List as Endangered (Self-Sullivan and Mignucci-Giannoni 2008). The subspecies is also considered Endangered by the Official Mexican Norm NOM-SEMARNAT-059–2001 (SEMARNAT 2010), and by the Belizean Wildlife Protection Act No. 4 (Government of Belize 2000). The distribution of the subspecies occurs from the Gulf of Mexico, the east coast of Mexico, Central America to the northeast of Brazil, including the Caribbean islands (Lefebvre et al. 2001; Quintana-Rizzo and Reynolds III 2010). The state of Quintana Roo (Mexico) offers relevant habitats for manatees, including among others, the river-lagoon systems, such as the Hondo River.

There are two genetically distinct manatee populations in Mexico: one found in the fluvial-lagoon systems of the Gulf of Mexico and another on the Caribbean coasts (Nourisson et al. 2011). In the case of Belize, manatees found in the Southern Lagoon form a genetically distinct population from the Belize City cays (Hunter et al. 2010), while Chetumal Bay and the Northern Belize coasts share a single population unit (Vianna et al. 2006) estimated to be made up of 90 to 130 individuals (Quintana-Rizzo and Reynolds III 2010; SEMARNAT 2018). Manatees that move along the coastline between Chetumal Bay and the coasts of Belize can cover distances of approximately 240 or 300 km (Castelblanco-Martínez et al. 2013; LaCommare et al. 2008).

Telemetry studies in the Mesoamerican region have demonstrated that manatees occupy marine and estuarine waters, but can also venture into some freshwater rivers such as the Belize and Hondo rivers (Castelblanco-Martínez et al. 2013; Morales-Vela et al. 1999). However, aerial surveys -which are widely accepted as the primary method to estimate the distribution, abundance and critical habitats for manatees in the Caribbean (Castelblanco-Martínez et al. 2019; Morales-Vela et al. 2000; Olivera-Gómez and Mellink 2005)- are typically restricted to coastal, shallow, and transparent waters. Therefore, the distribution, abundance, and habitat selection of manatees in fully freshwater environments of the Mesoamerican region have not been well investigated. In particular, the Hondo River is considered a traditional area for manatees, and the species have been reported in the first 6 km of the main channel of the river and in the Four Mile lagoon (Auil 2004; Colmenero-Rolón and Zárate 1990; Morales-Vela et al. 2000; O'Shea and

Salisbury 1991). Also, it is known that manatees move between Chetumal Bay, the mouth of the Hondo River, the Four Mile lagoon and the coasts of Belize (Castelblanco-Martínez et al. 2013; Morales-Vela et al. 1999).

The Hondo River is the natural border between Mexico and Belize, and a critical climatic and hydrological regulator of Chetumal Bay (Magnon-Basnier 2002). Despite its ecological importance, this river is not protected and faces strong environmental pressures including water contamination, land use change, invasive species, among others (Buenfil-Rojas and Flores-Cuevas 2007; Schmitter-Soto et al. 2015; Tun-Canto et al. 2017). Several ecohydrological characteristics influence the presence of manatees such as shallow depths, abundant aquatic vegetation, transparent waters and proximity to confluences (Jiménez-Domínguez and Olivera-Gómez 2014; Jiménez 2005; Morales-Vela et al. 2000; Olivera-Gómez and Mellink 2005; Puc-Carrasco et al. 2016). However, the degree to which these variables influence manatee distribution appears to be context dependent (Favero et al. 2020), and have not been investigated in the Hondo River.

Conservation strategies for an endangered species generally include the protection of the target species and its habitat. Thus, several countries have adopted the use of flag species for the creation of corridors or protected areas (Campbell 2017; Marsh and Morales-Vela 2011). On the other hand, the use of charismatic megafauna has proved to be an effective way to bring attention to broader conservation issues (Armstrong 2002; Lambeck 1997), and manatees in particular may serve as a sentinel species, reflecting the deleterious effects of polluted aquatic ecosystems (Bonde et al. 2004). Whether the long-term objective is to protect an endangered species or to use a charismatic or sentinel species to facilitate the habitat management, it is necessary to gather a basic site-specific understanding of the species distribution and habitat use (Packard and Wetterqvist 1986), including the identification of ecohydrology variables defining the space selection. Here, we investigate the ecohydrological variables influencing manatee presence and spatio-temporal habitat use in the Hondo River system, Quintana Roo (Mexico), to build a predictive model of manatee distribution. Thus, we aimed to compile formative baseline information on manatee habitat selection that

will be relevant to guide the decision process for Hondo River management and conservation.

Methods

Study area

The Hondo River is located in the state of Quintana Roo, Mexico, and belongs to the Chetumal Bay and other basins (RH33A) (INEGI 2017a), and to the Hondo River basin, in Belize (Meerman and Clabaugh 2017) (Fig. 1). The source of the river occurs in Guatemala and flows as a natural border between Mexico and Belize, discharging into Chetumal Bay. It is one of the main hydrological components of Chetumal Bay, contributing 1,500 mm³ of freshwater

per year, with a minimum flow of 20 m³/s in March and a maximum flow of 220 m³/s in July. Additionally, the Hondo River plays the role of a climatic and hydrological regulator as it is interconnected with wetlands, lagoons, cenotes and other bodies of water in the area (Magnon-Basnier 2002).

On average, the Hondo River is 10 m deep, 50 m wide and has a slope of 5° (Magnon-Basnier 2002). Most of the territory around the river is homogeneous in relief but contains a geological fault on its channel. The climate is warm sub-humid with summer rains, average temperature of 26 °C and average precipitation of 1,550 mm, but it is colder and drier in the upstream region (24 °C, 1,000 mm) and warmer and wetter near the mouth (28 °C, 1,500 mm) (Magnon-Basnier 2002). The riparian vegetation includes various types of rainforests: medium sub-deciduous, low

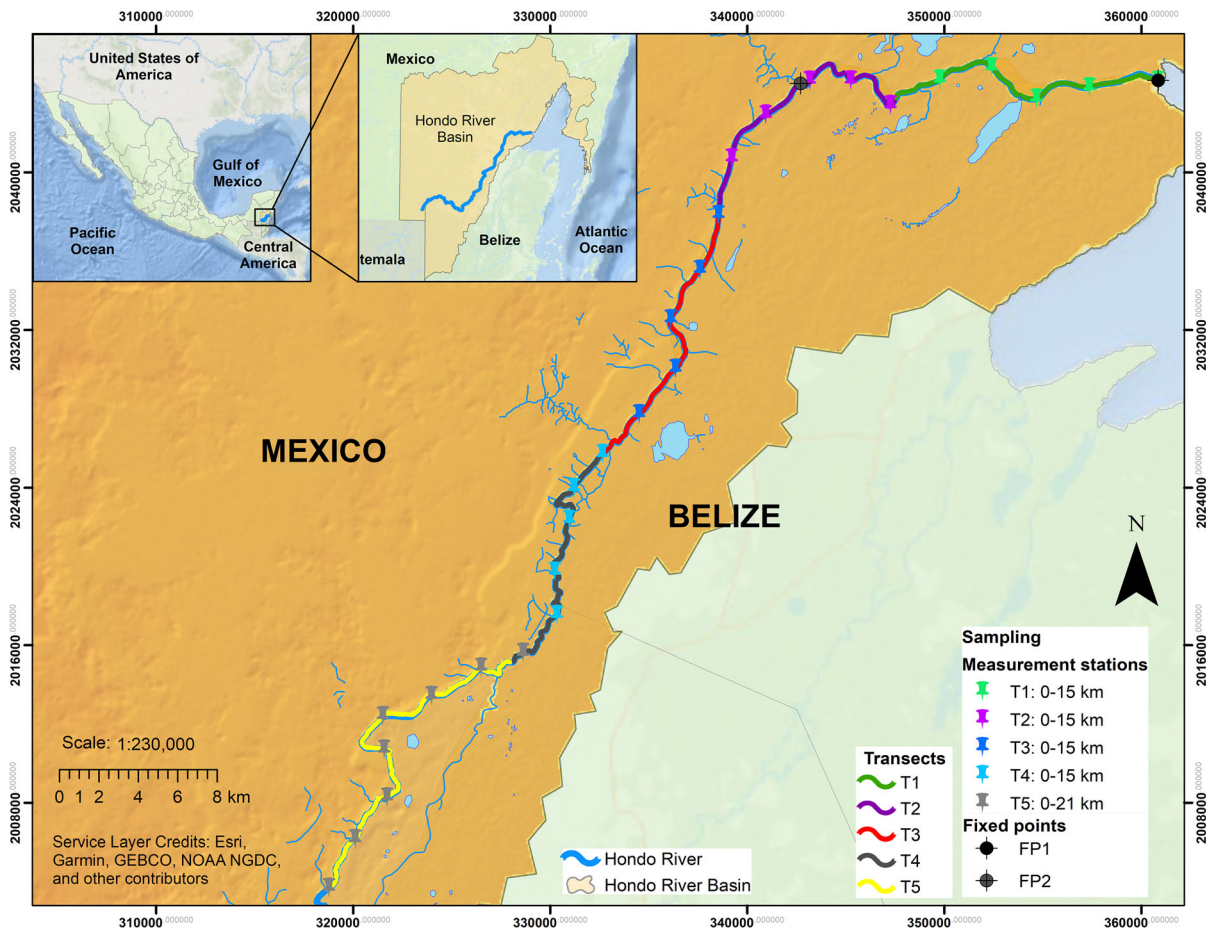


Fig. 1 Transects ($n = 5$) and ecohydrological variables measurement stations (every 3 km) assigned in the first 81 km from the mouth of the Hondo River. Two fixed-points for manatee observation are shown in T1 and T2

evergreen, low flood, savanna, reed beds, cultivated grassland and riparian mangrove (Granados-Sánchez et al. 1998; INEGI 2017b; Meerman and Clabaugh 2017). The dry season occurs from March to April, the rainy season from June to October and the 'Nortes' or windy season from October to February.

Manatee surveys

We used the following methodological approaches in order to record manatee presence: (1) side-scan sonar detections (Fig. 2), (2) sightings during boat-based surveys, at fixed points, or opportunistic and, (3) indirect evidence (feces). The first 84 km of the river was divided in four transects of 15 km long and the last of 21 km long (Fig. 1). Each transect was surveyed in a 7 m-length boat equipped with a

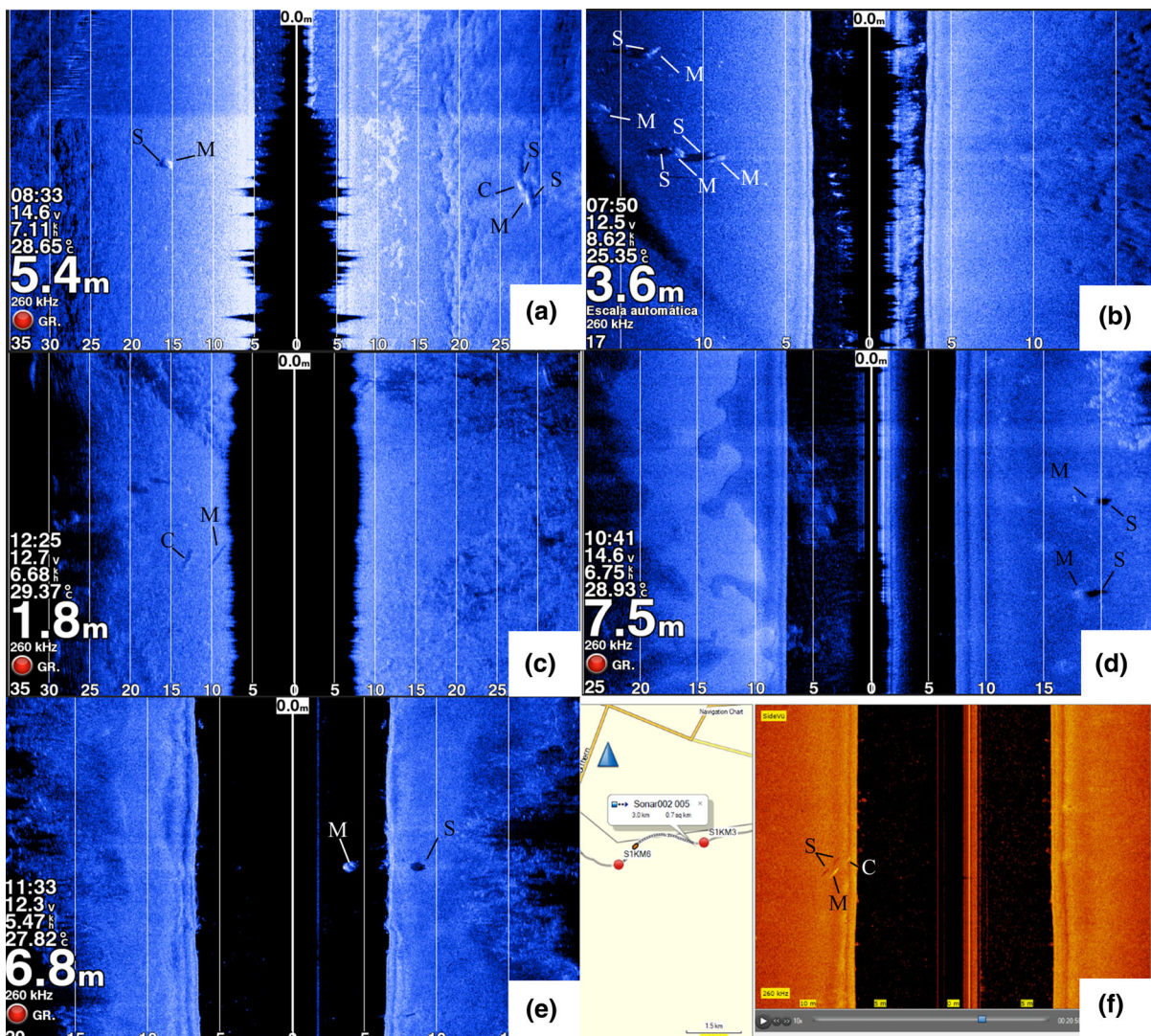


Fig. 2 Manatees detected by side-scan sonar method. Image symbols: manatee (M), calf (C), shadow (S). **a** mother-calf dyad at T1km0 (river mouth) in June 2018, confirmed in the field; **b** group of four manatees at T1km0 in February 2018, confirmed in the field; **c** mother-calf dyad in T2km6 in May 2018,

confirmed in the field; **d** two manatees in T3km9-12, in June 2018, according to expert consultation; **e** manatee at T5km15 in April 2018, confirmed in the field, and **f** two manatees detected during the sonar recordings analysis, at T1km3-6, in March 2018

60 HP 4-stroke outboard motor. The navigations were conducted at 7.0–8.0 km/h at the middle and deepest area of the river channel and following the shoreline. Each transect was sampled once a month during November 2017, and from January to June 2018, covering ‘Nortes’ and dry seasons. The first two transects were sampled in a single day, to reduce the error of double counts of manatees, due to the antecedent that they have been observed mostly at these sites.

The boat was equipped with a side-scan sonar unit (GARMIN echomap 74sv, 500 W power) configured to sweep the area at a 30 m side width and a 260 kHz frequency. The crew consisted of a captain and at least two observers. One observer oversaw the side-scan sonar (SSS), while the other searched for visual clues of manatees or their feces. If a shape suggesting the presence of a large animal was detected in the SSS monitor, we proceeded to pass through the same site twice to confirm if the object corresponded to a manatee (Arriaga-Hernández 2013). After a potential detection in the SSS, the observers tried to visually confirm manatee presence by detecting the exhibition of back, tail or snout above the water; as well as bubbles, sediment and formation of wakes typically left by manatees. From each potential SSS detection - confirmed in situ or not- a screenshot was taken to record ancillary information and the size of the object. The images captured and the recordings of each trip were selected according to the profile, shape, and size of a manatee, using an image viewer and the Home-Port program (Garmin).

Additionally to the boat-based surveys, visual surveys were conducted from fixed points using the anchored vessel as a floating observation platform (Morales-García 2013). The first fixed point (FP1) was located at the Hondo River mouth, and the second (FP2) at the confluence between the Ucum and Hondo rivers. FP2 observations were only made during the dry season. The fixed-point surveys consisted of silent waits of approximately 20 min searching for manatees at 360°. An effective sighting was considered when the manatee’s back, tail or snout was observed. When conditions allowed, an overflight was performed with a light drone (Phantom 3 model, with integrated GPS and 12.4 MP camera); flying at less than 50 m height and variable bandwidths, to confirm the sightings and to count individuals (Landeo-Yauri et al. 2020; Ramos et al. 2017). Class ages were assigned when possible:

two animals swimming together, one being approx. $\leq 2/3$ the length of the other, was considered a mother-calf dyad. The side-scan sonar images also allowed to distinguish between calves and adults in several opportunities (Fig. 2). The presence of feces was considered indirect evidence of manatee occurrence, and assumed as the record of one indeterminate individual, based on the fact that feces were found at a relative long distance from each other (> 1 km), and on different transects and sampling days. Whenever they were found, fecal samples were collected, conserved in the Laboratory of Biology and Molecular Ecology of the University of Quintana Roo, and used for a parallel study on manatee feeding ecology (see Arévalo-González 2020).

Ecohydrological variables were assessed every three kilometers along each transect, and every time the presence of a manatee was confirmed or suspected. The measured variables were temperature (°C), conductivity (mS/cm), transparency (m), depth (m), distance to the nearest tributary river (m), distance to the Hondo River mouth (m) and distance to land (m). Temperature and conductivity measurements were assessed using a multiparameter probe; the transparency using a Secchi disk; and depth and coordinates using the side-scan sonar. The land use was determined as follows: we created buffer zones of the length of each transect and 400 m width at each margin of the river, and categorized each of them according to the land use type as: mangrove, medium sub-evergreen forest, low sub-perennial forest, tular, savanna, annual and semi-permanent seasonal agriculture, cultivated pastures, and settlements. The land use information layers were obtained in vector format for the year 2017, from the online platforms of the National Institute of Statistics and Geography (INEGI) and Biodiversity & Environmental Resource Data System of Belize.

The main tributary lagoons, rivers, and other hydro-geographic features of the study area were georeferenced. Each selected water body was named in accordance to the nomenclature of the Mexican water network (INEGI 2017a), by the closest locality, or according to the references provided by local people: Boca (mouth), Four Mile, López (Subteniente López), Chac (Estero Chac), Ucum, Diablo (river of the Curva del Diablo) and Román (river of the village of San Román). Other influential variables considered for the analyzes included precipitation (mm), obtained in the

databases of the National Meteorological Service of Mexico, and bottom type detected by the side-scan sonar and coded as: mangrove (1), dense grasses (2), scattered grasses (3) and silt substrate (4) (González-Socoloske and Olivera-Gómez 2012; McLarty et al. 2019). For analytical purposes, ecohydrological variables were classified as temporal (temperature, conductivity, and transparency) and non-temporal variables (depth and distances to land uses, river, and mouth), the latter showing little variation among the months of sampling.

Data analysis

A relative abundance index (RAI) was used as an indicator of space use by manatees (Castelblanco-Martínez et al. 2017), and was calculated as the sum of all the evidence types found (SSS detections -those confirmed in the field, corroborated with literature and expert consultation-, direct sightings, opportunistic records, and feces) by kilometer navigated (for boat-based surveys) or by minute (for fixed points). For both cases, the RAI was estimated also by sampling time. To estimate the manatee population size in the Hondo River, we used a modified N-mixture model for spatial replications proposed by Royle (2004), using the transect-specific function of *pcount* from the unmarket library (Fiske and Chandler 2011) in the R program (RCoreTeam 2018). The model was parameterized according to the transect-based sampling design (e.g., transect-specific model), where each 15-km transect was assumed as a sampling location, and the monthly counts were considered as a sampling occasion with a count table of 5×7 dimensions.

The N-mixed model assumes that the study population is closed, that is, no mortality, recruitment, or migration occurs (Royle 2004). Furthermore, the model considers double-counting, i.e., movement between transects or recruitment, as one of the sampling errors. Given that this study is one-off and only considers a short sampling period, we consider it plausible to assume that the manatee population of the study area is closed. In other words, we assume that, at this short scale, processes determining the long-term population dynamic (e.g., mortality, recruitment, migration) are not affecting our results.

Temperature, transparency, and conductivity variables were transformed through a principal component analysis to avoid collinearity in the model. The

components were included as explanatory variables to model the probability of detection. Abundance was only modeled on the intercept. Models were adjusted with Poisson distribution and negative binomial that considered the over dispersion. These distributions have been used in previous studies to estimate the population abundance, distribution and habitat use of manatees (Jiménez-Domínguez and Olivera-Gómez 2014; Jiménez 2005). The used integration parameter k is equal to the number of transects multiplied by the temporal samples ($k = 35$). We estimated the population size as the sum of the estimated abundances by transect. The following ecohydrological variables were used as predictor variables ($p = 21$) for the manatee-presence estimation model: transparency, depth, temperature, conductivity, distance to rivers, distance to the mouth, distance to the use of land, and coordinates. To identify the relative importance of each ecohydrological variable, an ordinal classification model (0–4 manatees) was adjusted with the random forest method, using the *randomForest* function (Liaw and Wiener 2002) of the R program.

The model was generated with 500 classification trees and four variables for each partition selected. The Gini index was used to assess the contribution of the predictor variables and to identify the most important variables, e.g., with the highest predictive power. The quality or robustness of the model was evaluated based on the AUC (Area Under the Curve) statistic or area under the ROC curve (Receiver Operating Characteristics), which assesses the ability of the model to correctly classify the species as present or absent (pseudo-absence) (Hanley and McNeil 1982). The AUC value ranks between 0 and 1 (0–100%), with values between 0.7 and 0.9 corresponding to good models and values greater than 0.90, to very good models (Peterson et al. 2011). The curve was contrasted between absences (value = 0) and presences (values ≥ 1) of manatees. The ROC curve was performed with the *pROC* package (Robin et al. 2011).

We used the following data to estimate the population size and to predict the likelihood of manatee presence: SSS detections (confirmed in the field, corroborated with literature and expert consultation), direct sightings during boat-based surveys, and direct sightings from fixed points. We used the records of manatee absence and sightings in the seven-month sampling period to build the distribution model, considering the observations as independent records.

Since the random forest model could overestimate the population, it was not used to estimate the manatee population size.

A map of probability distribution of manatee presence was created, and continuous raster maps were generated for each temporal and non-temporal ecohydrological variable used in the random forest model. The random forest algorithm was also applied for the construction of continuous maps through interpolation and, in this case, the predictor variables were the geographic coordinates. Coordinates were included for the map of non-temporal variables (depth, land use and bottom type). The maps of the temporal ecohydrological variables (conductivity, temperature, and transparency) included the variable ‘month’ as a factor and other influential variables such as precipitation, bottom type, depth, land use and distance to tributary rivers.

Results

The sampling effort totaled 136.50 h, and the total operating effort using the side-scan sonar was 528 km. The temperature varied from 24 to 32 °C, with the highest value recorded in May and the lowest in January during the windy (‘Nortes’) season. The conductivity values ranged from 1.01 to 2.23 mS/cm with highest values recorded mainly in June. The lowest transparency values were recorded in November, February, and March. Although the depth was quite similar in all the months, the lowest depth recorded was 2.30 m and the deepest was 12.70 m. The most represented land use type was the tular (52%), followed by the mangrove forest (17%), low sub-evergreen forest (9%), agriculture (9%), medium sub-evergreen forest (8%) and settlements (4%); the least represented (1%) were cultivated pastures, savanna and others.

A catalog was made of 146 selected side-scan sonar images, which were evaluated by experts in the use of sonar applied to manatee research (Fig. 2). Confidentiality values were assigned to each observation (sensu Castelblanco-Martínez 2014) to discard false positive images. Seventeen images were approved by experts and included for analysis. One-hundred and twenty-three manatees were sighted during boat-based surveys (47%), fixed points (29%), and opportunistically (24%). Additionally, 10 samples of manatee feces

were found, mostly (70%) in the first two transects of the river. Of the 133 manatees’ records (123 observations plus 10 feces), 45% correspond to adults, 16% to calves and 39% to indeterminate (Table 1). Adult and indeterminate individuals were observed in all transects of the river (except for the fourth), mainly in the dry season; while calves were only observed in the first three transects (Table 1).

The group size was one (51%), two (34%), three (11%) or four (4%) individuals. The highest RAI occurred during the dry season. As for the fixed points, the RAI at the mouth was greater in the dry season. The mean RAI for the transects in the ‘Nortes’ and dry seasons was 0.07 and 0.16 manatees, respectively (Table 2). The estimated manatee population size for the sampled channel, according to the Akaike Information Criterion (AIC = 151), was 51 individuals (Table 3). The average manatee abundance was greater in the first transect, for the three models compared, and decreased in transects furthest from the mouth. The fourth transect presented the lowest abundance of manatees, according to the three models. There was a positive effect of principal components 1 ($B = 0.72$, $p < 0.0001$) and 2 ($B = 0.70$, $p < 0.0001$) in relation to the probability of manatee detection in the model, indicating that as conductivity and transparency increase in component one, the probability of detecting manatees increases. Likewise, as the temperature in component 2 increases, the probability of detection increases (Fig. 3). The probability of manatee detection tended to increase in May and June, with transect 1 having the highest likelihood of manatee detection (Fig. 4).

The random forest model determined an estimated error rate (OOB) of 26%. Of the total number of records ($n = 268$), the model classified 69 records incorrectly (Table 4). That is, the random forest model will be 18% wrong in predicting the presence of manatees. The obtained model showed that the efficiency of predicting manatee presence or absence is within the AUC range (ROC curve), which is set from 0.76 to 0.97. The AUC was 0.9257, indicating a very good precision of the model according to Peterson et al. (2011). According to the Gini index (G), the ecohydrological variables with the highest predictive power were: conductivity ($G = 8.5$), temperature ($G = 8$), and depth ($G = 7.2$), followed by distance to Curva del Diablo ($G = 6.5$), transparency ($G = 6.3$), distance to pastures (6.2) and distance to

Table 1 Direct sightings (adults, calves or indeterminate) and indirect evidences (feces) of manatees obtained during boat-based surveys (transects 1–5) and fixed points (FP1 and FP2)

Season	'Nortes'					Dry					Total
	Adults	Calves	Indet	Feces	Total	Adults	Calves	Indet	Feces	Total	
Transect1	13	3	4	2	22	21	7	19	2	49	71
Transect2	0	0	0	0	0	3	2	3	3	11	11
Transect3	0	0	3	0	3	1	1	2	1	5	8
Transect4	0	0	0	0	0	0	0	0	1	1	1
Transect5	2	0	0	0	2	1	0	2	1	4	6
FP1	4	2	1	0	7	13	6	7	0	26	33
FP2	–	–	–	–	–	2	0	1	0	3	3
Total	19	5	8	2	34	41	16	34	8	99	133

Indet = indeterminate

Table 2 Relative Abundance Index (RAI) of manatees by season and survey type

Effort = Sampling effort was defined as distance surveyed (kilometers) for transects, and as waiting time (minutes) for fixed points. # Est. Ind. = Estimated individuals. Dash lines indicate no effort

Season	'Nortes'				Dry			
	Effort	Sightings	RAI	# Est. Ind	Effort	Sightings	RAI	# Est. Ind
Transect1	45.00	12	0.27	3	60.00	33	0.55	18
Transect2	45.00	0	0.00	0	60.00	8	0.13	1
Transect3	45.00	2	0.04	0	60.00	3	0.05	0
Transect4	30.00	0	0.00	0	60.00	1	0.02	0
Transect5	42.00	2	0.05	0	84.00	3	0.04	0
FP1	220.00	5	0.02	0	340.00	11	0.03	0
FP2	–	–	–	–	260.00	3	0.01	0
Mean (T1–T5)	41.40	3	0.07	1	64.80	10	0.16	2
Mean (FP)	220.00	5	0.02	0	300.00	7	0.02	0

Table 3 Estimation of population size and average manatee abundance by transect in the Hondo River, according to the Null, Poisson, and Negative Binomial models. Confidence interval is 95%

Transects	Null AIC: 273.68			Poisson AIC: 151.22			N. binomial AIC: 183.26		
	Mean	LL	UL	Mean	LL	UL	Mean	LL	UL
Transect1	34	32	35	34	32	35	34	31	35
Transect2	11	10	13	11	10	12	13	10	16
Transect3	5	3	7	4	3	7	12	7	18
Transect4	1	0	3	0	0	1	6	2	11
Transect5	3	2	6	2	2	4	12	7	18
Total	54			51			77		

savanna, San Román and mouth ($G = 6.2$). The variables with intermediate importance ($G = 3.8–5.0$) are coordinates, the distance to the mangrove areas, agriculture, the Four Mile lagoon. The least important ($G \leq 3.7$) were the distance to the Subteniente López and Ucum rivers, and the distance to the sub-evergreen median rainforest. The greatest

probability of manatee presence occurs in transect 1 and decreases upstream. However, in transects 2, 3 and 5, conditions in certain areas are potentially predictive for manatee presence. The model predicts the lowest probability of detecting manatees in transect 4 (Fig. 5).

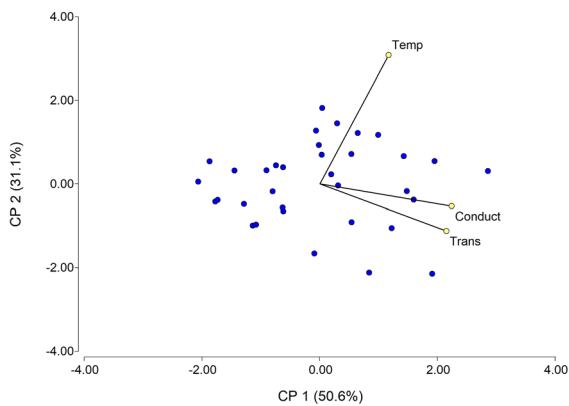


Fig. 3 Principal component analysis for the explanatory variables (temperature, conductivity, and transparency), and the probability of manatee detection

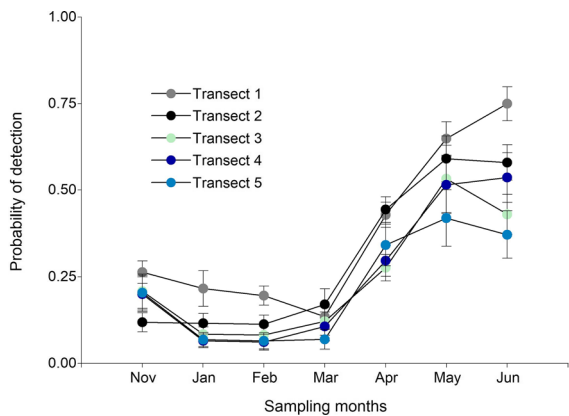


Fig. 4 Inter-monthly temporal variation of manatee detection probability according to the Poisson model

The principal component analysis showed that the first component (CP1) separates conductivity, transparency, distance to the mouth, the Four Mile lagoon and the mangrove forest from the distances to the San Román and Curva del Diablo rivers, the savanna and pastures (Fig. 6). Component 2 separates the variables of depth and distance to agricultural soil. Both

components (CP1 and CP2) explain 71% of the total variability of the ecohydrological variables. Thereby, high values of conductivity and transparency and shorter distances to the mouth, the Four Mile lagoon and the mangrove forest are associated with the higher probabilities of manatee presence, while the proximity to the rivers of the Curva del Diablo and San Román and pastures, savanna and agriculture are conditions mostly associated to the absence of manatees. Also, greater water depths were associated with the absence of manatees; the temperature showed no association with the presence or absence of manatees in these first two axes.

Discussion

Observing manatees in continental waters with low transparency as those of the Hondo River is challenging, and the most efficient and productive approach seems to be to use all evidence types (Castelblanco-Martínez et al. 2017). Several studies have used statistical models, such as binary logistic regressions, Bayesian, generalized linear models (GLMs) and multivariate to estimate the presence and population size of manatees based on habitat characteristics (Guzmán and Condit 2017; Jiménez-Domínguez and Olivera-Gómez 2014; Jiménez 2005; LaCommare et al. 2008; Martin et al. 2014). One of the advantages of the random forest model, used in this study, is that it evaluates the contribution of each predictor variable independently, that is, without modifying the others (Cutler et al. 2007).

Solitary individuals were observed in all transects of the river, but only indirect evidences (feces) were found in the fourth transect. Mother-calf observations were more frequent in the first transect, as reported in the studies by Campbell and Gicca (1978), Bengtson and Magor (1979), Fuentes Allen and Aguayo Lobo

Table 4 Confusion matrix of the random forest model that predicts the presence of manatees in the Hondo River

	Counts: absences (0) and presences (1–4 individuals)					Error classes
	0	1	2	3	4	
0	186	6	3	0	0	0.05
1	20	9	4	3	0	0.75
2	12	6	4	3	0	0.84
3	2	3	3	0	1	1.00
4	2	0	1	0	0	1.00

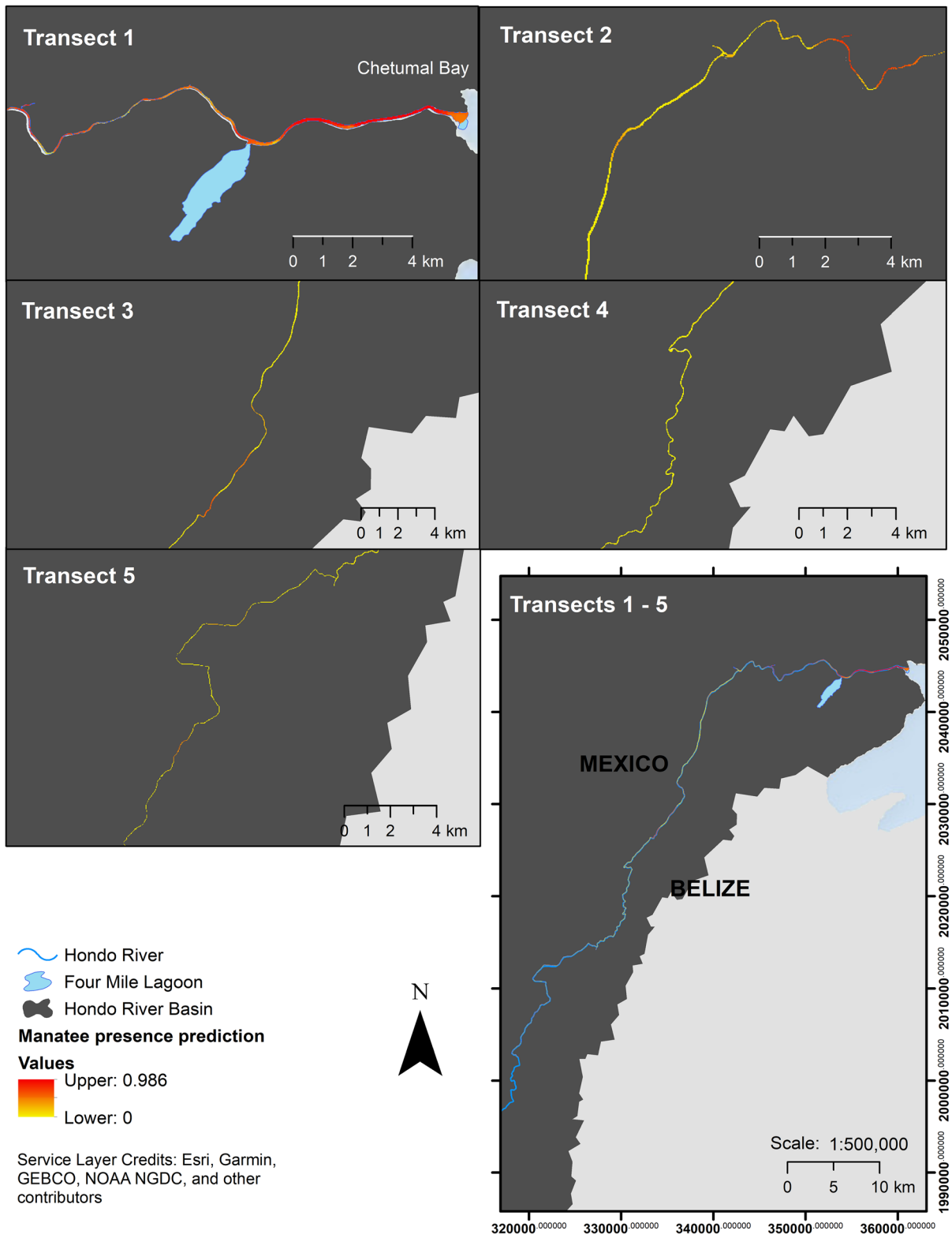


Fig. 5 Predictive models of manatee presence in the Hondo River, Quintana Roo, Mexico

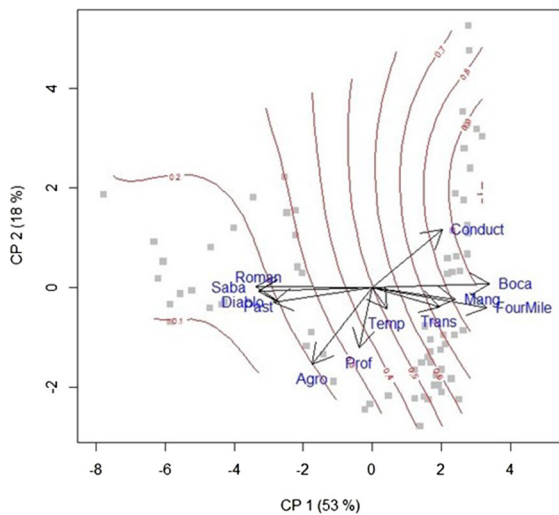


Fig. 6 Biplot for relevant ecohydrological variables, and their relationship with the likelihood of manatee presence (red lines). Gray squares correspond to the 268 manatee records used to estimate the probability of manatee detection in the river

(1989), Colmenero-Rolón and Zárata (1990), O’Shea and Salisbury (1991), Zárata Becerra (1993) and Auil (2004), in the Hondo River. The RAI reflected more records of manatee observations in the transects closest to the mouth. Several studies indicate higher relative abundances in semi-open water systems than on the coasts (Axis-Arroyo et al. 1998) or in sites with more complex or heterogeneous habitats, which have confluences between river-lagoon systems, than in homogeneous sites (Auil 2004; Morales-Vela et al. 2000; Puc-Carrasco et al. 2016).

The estimate of the manatee population size in the river is proportionally similar to other water systems with similar environmental conditions, such as Tabasco, with 28 manatees for a fluvial-lagoon system of around 14 km (Puc-Carrasco et al. 2017) and 18 manatees for an 18 km river in Bocas del Toro, Panama (Guzmán and Condit 2017). In this study, the population size was estimated assuming a closed population; however, this population could be considered open, since there is enough evidence of manatee movements between Chetumal/Corozal Bay and the coasts of Belize (Castelblanco-Martínez et al. 2013; Morales-Vela et al. 1999), with manatees showing a movement rate of 0.13 km/h (Castelblanco-Martínez 2010). Breeding manatee females often have fidelity patterns to specific sites (Deutsch et al. 2003; Gannon et al. 2007; Morales-Vela et al. 1999; Powell and

Rathbun 1984; Rathbun et al. 1990). The constant observations of female-calf pairs in the first transects of the Hondo River could indicate that those are important nursing areas for manatees.

The peak of manatee detection occurred during the dry season, mainly in May and June, for all the study area including the furthest ones. Similar results were reported for Belize (Auil 2004) and for French Guyana (Castelblanco-Martínez et al. 2017). In contrast, Morales-Vela et al. (2000) reported low abundance of manatees in rivers and lagoons during the dry season, while in the bay the abundance was higher. Our results suggest that manatees living in saline environments move toward continental waters to cover their need for freshwater. Thus, manatees moving around Chetumal Bay or north of the coastal zone of Belize can supply their freshwater needs in the first transects of the river during the wet season. In the dry season, when the plume of salinity enters the Hondo River, they need to move further upstream where the salinity is lower or null. This strategy of remaining near freshwater sources seems to be advantageous in terms of energy investment (Olivera-Gómez and Mellink 2005).

The Hondo River habitat shows appropriate conditions for manatees. The most important ecohydrological variables explaining the manatee presence were those related to the characteristics of the river (conductivity, temperature, depth, and transparency), while bank characteristics were less important. The Hondo River has several tributary rivers along its channel that differ from each other in length, width, and depth, apart from those referenced in this study. Several of these confluences are found in the classified transects, which is why they offer heterogeneous conditions that favor the presence of manatees (Jiménez-Domínguez and Olivera-Gómez 2014; Puc-Carrasco et al. 2016). Although our results suggest a preference by the transects near the mouth, we present clear evidence that the species also use the upper transects of the Hondo River. In fact, several feces were found upstream, and although we have no evidence of feeding in this study, the area offers riparian vegetation, e.g., submerged grasses, mangrove (*Rhizophora mangle*), water hyacinth (*Eichhornia crassipes*), for the species (this study, Arévalo-González 2020).

The model estimated probabilities, although low, of manatee presence in transects 3–5. The fourth transect

was the one that presented the lowest probability values, which may be due to the fact that the environmental conditions in this area are less favorable for manatees (greater depths, low transparencies), in addition to being the most homogeneous (presence of tular as dominant land use), compared to the other transects of the river. The characteristics of the first transects are related to the presence of mangrove forest, dense pastures on the bottom, proximity to the Four Mile lagoon, clear waters with high values of conductivity and relatively low depths, which make an attractive environment for manatees. Indeed, these conditions offer shelter, feeding resources, and resting areas, which has been proven by previous authors as important requirements for manatee space selection (Fuentes Allen and Aguayo Lobo 1989; Jiménez-Domínguez and Olivera-Gómez 2014; Morales-Vela and Olivera-Gómez 1997; Morales-Vela et al. 2000; Olivera-Gómez and Mellink 2005; Puc-Carrasco et al. 2017, 2016).

Water conductivity showed higher values in the lowest section of the river and this may be explained by the proximity to the mouth, i.e., to the most saline environment. Water salinity can influence manatee distribution: The species prefers fresh or brackish waters; thus, manatees are found in areas close to water-bodies that provide fresh water (Hartman 1979; Olivera-Gómez and Mellink 2005). There is evidence of a positive correlation between plant biomass/cover in Mesohaline habitats and the water conductivity/salinity (Olivera-Gómez and Mellink 2005, 2013). Although we did not measure aquatic vegetation biomass, areas associated predominately with mangrove (e.g., *R. mangle*) represent a rich offering of food resources for manatees including dense sub-aquatic vegetation beds (*Ruppia maritima*, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Najas marina*, *Chara* sp., *Batophora* sp.) (Arévalo-González 2020; Espinoza-Ávalos 1996; Espinoza-Ávalos et al. 2009; LaCommare et al. 2008; Zárate Becerra 1993), which have been reported as part of the manatee diet (Castelblanco-Martínez et al. 2009; Marsh et al. 2011; Mignucci-Giannoni 1998).

The model also indicated that transparency influences the presence of manatees, mainly because this variable has a positive effect on other variables such as the presence of subaquatic vegetation (Jiménez-Domínguez and Olivera-Gómez 2014; Jiménez 2005). Also, even though other studies indicated that

the water transparency itself does not have an important influence on habitat selection (Auil 2004; Hartman 1979), it may have a critical effect on our capacity to visually detect manatees; especially when we are relying on boat and drone-based surveys. Although the water temperature was one of the important variables for the model, it did not show a clear trend in relation to the probability of observing manatees. This can be explained by the fact that in tropical waters, temperature is not a determining factor in the distribution of manatees, since it is relatively constant and exceeds 20 °C which is critical for manatees (Axis-Arroyo et al. 1998; Irvine 1983; Jiménez 2005).

In the Hondo River, previous research has demonstrated the presence of high levels of heavy metals and organochlorine compounds, derived mainly from the agrochemicals and pesticides used in the cane crops nearby (Buenfil-Rojas and Flores-Cuevas 2007; González Bucio et al. 2013; Tun-Canto et al. 2017). It is necessary to include an ecohydrological approach in the management policies of the banks of the Hondo River and, if possible, at the basin level, to ensure the long-term sustainability of the river-lagoon ecosystem, considering that water resources are part of the functional and interrelated complex systems and all its components and levels (Zalewski 2006). In addition, including a target, charismatic species as the manatee as the core of management plans may facilitate the maintenance of safe ecological conditions, and the biological integrity of the Hondo River fluvial-lagoon ecosystem (Armstrong 2002; Lambeck 1997).

Manatees are completely herbivorous and considered nutrient recyclers (Castelblanco-Martínez et al. 2012), they contribute to the population growth control of aquatic plants and provide nutrients to submerged grass beds through their feces, benefiting the aquatic ecosystem (Etheridge et al. 1985; Reynolds III et al. 2002). The manatee is an endangered marine mammal occupying the Coastal Transverse Corridor of southern Quintana Roo (Hernández-Arana et al. 2015), a critical area for the hydrological regulation of the region. We recommend considering at least the first 30 km of the river as part of the protected areas of the Chetumal Bay Manatee Sanctuary, in Mexico, and the Corozal Bay Wildlife Sanctuary, in Belize. Although the passage of high-speed motorized boats in the river was not evidenced in this study, this is a potential threat to manatees that could increase in the following years. For these reasons, the speed

regulation of the boats transiting in the riverbed should be considered within the management actions.

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Author contributions MFC-F, DNC-M, NR, and CAN-T designed the project. MFC-F collected the data; MFC-F, SV-M, DNC-M and NR interpreted data. All authors undertook a first critical revision of the manuscript and approved the final version for publication.

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Data availability We will upload the research database on an online platform, for interested researchers to access all data, prior to the request of the corresponding author.

Compliance with ethical standards:

Conflicts of interest All the authors declare that there is no conflict of interests.

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