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Use of aerial surveys for assessing abundance of the whale shark (*Rhincodon typus*) and the giant manta (*Mobula birostris*) in the northern Caribbean Sea off Mexico

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Abstract—The whale shark (*Rhincodon typus*) and the giant manta (*Mobula birostris*) are migratory species that occasionally occur in the same foraging habitat. Both planktotrophic elasmobranch species can be found seasonally in aggregations from 2 individuals to hundreds of animals in the northern Caribbean Sea off the Yucatan Peninsula of Mexico because of the abundance of food in this area. The aim of this study was to assess the distribution and abundance of the whale shark and giant manta by conducting aerial surveys from May through September during 2016–2018. A total of 953 whale sharks and 466 giant mantas were sighted during 17 aerial surveys. The largest groups of whale sharks and giant mantas were recorded in July 2017 and September 2016, respectively. Aerial survey data were used to estimate the mean density of each species in this aggregation area: 14 whale sharks/100 km^2 and 8 giant mantas/100 km^2. These values were used to estimate the spatiotemporal variability of the number of whale sharks and giant mantas feeding at the surface. The results of this study indicate that both species were not distributed homogeneously in the assessed area, a situation that often interferes with the implementation of suitable strategies for managing tourist activities.

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In the northern Caribbean Sea off the Yucatan Peninsula in southeastern Mexico (Fig. 1), whale sharks (*Rhincodon typus*) form seasonal aggregations from May through September. The number of individuals and distribution of whale sharks near the sea surface is highly dynamic, varying among seasons, days, and hours (de la Parra Venegas et al., 2011; Cárdenas-Palomo et al., 2015). The waters of the Caribbean Sea off the northeastern coast of the Yucatan Peninsula is one of the most important aggregation sites for whale sharks, with the largest number of individuals identified to species by using photographs; between 1999 and 2015, 1115 whale sharks were recorded in the Wildbook Whale Shark photo-identification database (available from website) (McKinney et al., 2017; Norman et al., 2017). In addition, in the northern Caribbean Sea off Mexico there are aggregations of giant mantas (*Mobula birostris*), whose population size, movement patterns, and ecology are poorly known (Graham et al., 2012). The productivity in this region is high because of the upwelling on the Yucatan Shelf that fertilizes the ecosystem with nutrients rising from deep waters, enriching marine habitats, and providing food for many species (Merino, 1997; Reyes-Mendoza et al., 2016).

Since 2004, tourism related to whale sharks has increased exponentially, and it is currently a significant source of income for communities near the feeding sites of this species on the northeastern coast of the Yucatan Peninsula (Mimila-Herrera et al., 2016); these communities also use giant mantas as tourist attractions and their meat as bait (Hinojosa-Álvarez, 2009; Graham et al., 2012). Therefore, information about ecological characteristics of these species is needed for their management in this region. To that end, we conducted aerial surveys between 2016 and 2018 to

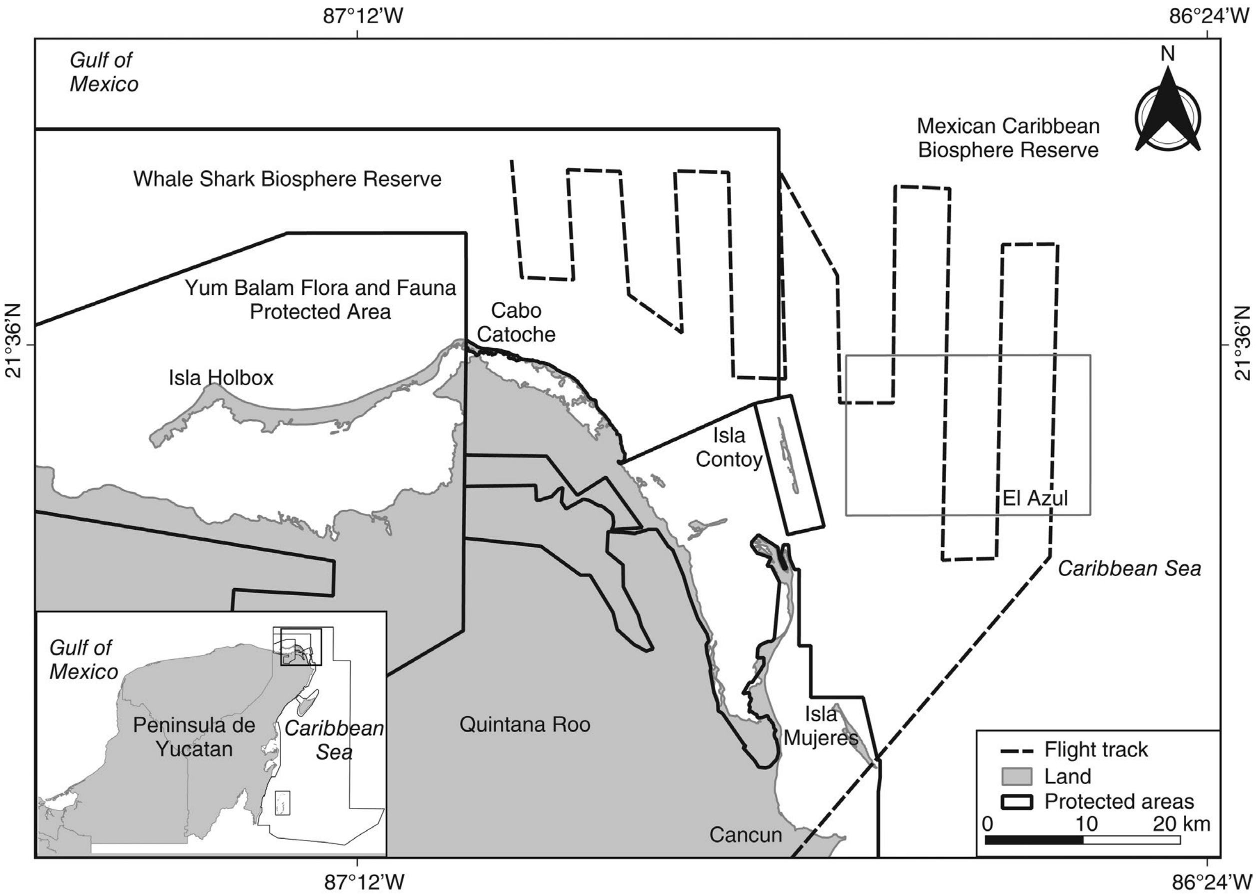

Figure 1

A map of the study area where aerial surveys of whale sharks (*Rhincodon typus*) and giant mantas (*Mobula birostris*) were conducted in the Caribbean Sea off the northeastern coast of the Yucatan Peninsula of Mexico between May and September during 2016–2018. The flight track (dashed line) was designed to cover the major area of aggregations of whale sharks and giant mantas in the region, which includes zones of high abundance of these species in the Whale Shark Biosphere Reserve (outlined with black lines along with other protected areas) and in the Azul area (box outlined in gray), located in the Mexican Caribbean Biosphere Reserve. Surveys were conducted at an average altitude of 380 m above sea level and at a mean speed of 175 km/h. The survey transect had a length of 300 km.

assess the distribution and abundance of whale sharks and giant mantas and to estimate the spatiotemporal variability of the density of these species in the northern Caribbean Sea off Mexico.

Materials and methods

The study area is located in the Caribbean Sea off the northeastern coast of the Yucatan Peninsula, a location where previous research has identified 2 major areas with high abundance of whale sharks (Cárdenas-Palomo et al., 2015): the Whale Shark Biosphere Reserve (WSBR), a protected area decreed on 2009 (DOF, 2009), and a zone called the Azul, which is inside of the Mexican Caribbean Biosphere Reserve (MCBR), decreed in 2016 (DOF, 2016) (Fig. 1). The WSBR has high concentrations of chlorophyll-*a* (>1 mg/m^3), due to the influence of nutrient-rich waters from the Yucatan upwelling system, and a zooplankton biomass of approximately 103.5 mg/m^3 composed mainly of copepods, appendicularians, and chaetognaths (Merino, 1997; Cárdenas-Palomo et al., 2015; Reyes-Mendoza et al., 2016). The WSBR has an average depth of 12 m and an average sea-surface temperature during the rainy season of 26.2°C (Cárdenas-Palomo et al., 2015; Hacohen-Domené et al., 2017). The Azul area is characterized by oligotrophic conditions, such as waters with low levels of nutrients and low concentrations of chlorophyll-*a* (<1 mg/m^3) (Cárdenas-Palomo et al., 2015). In this area, the average depth is approximately 30 m, the sea-surface temperature in the raining season is 27.8°C, and zooplankton have a biomass >3356.1 mg/m^3 and consist mainly of fish eggs (Cárdenas-Palomo et al., 2015). The most numerous aggregation of whale sharks

Figure 2

Photograph of whale sharks (*Rhincodon typus*) and giant mantas (*Mobula birostris*) taken in September 2016 during an aerial survey along a transect in the Azul area, a zone of high abundance of these species in the Mexican Caribbean Biosphere Reserve. Photograph by E. Mimila-Herrera.

ever recorded was observed in the Azul area (420 individuals; de la Parra Venegas et al., 2011), and this area is also considered a core foraging location for giant mantas (Graham et al., 2012).

Aerial surveys

From 2016 through 2018, aerial surveys were conducted between May and September with a Cessna 206[1] high-wing aircraft (Textron Aviation, Wichita, KS). Each flight followed the survey transect shown in Figure 1 and was conducted at an average altitude of 380 m above sea level and at a mean speed of 175 km/h. In the northern Caribbean Sea off Mexico under appropriate climatic conditions, whale sharks and giant mantas can be clearly identified from as high as 579 m above sea level (Rowat et al., 2009).

The survey transect was designed to cover the major area of aggregations of whale sharks and giant mantas in the Caribbean Sea off the northeastern coast of the Yucatan Peninsula, and the transect had a mean length of 269 km. The mean duration of surveys was 165 min, and surveys were conducted from 0730 to 1130 or from 1500 to 1800. Because flight times varied, we standardized the results by reporting relative abundance and density, as well as the number of individuals sighted.

For the aerial surveys, an observer was positioned on each side of the airplane. The observers recorded the number of whale sharks and giant mantas observed and their geographical location with GPS. To reduce observer bias, the same 2 people conducted all aerial surveys, and each spotter sat in the same place of the plane. The observers were experienced in identifying marine megafauna from aerial flights by previously examining photographs taken during flights. Additionally, selecting appropriate survey days, based on sea state and weather conditions, made it easier for observers to locate and identify animals (Fig. 2).

For this study, no tests were conducted to estimate the range of lateral vision from the aircraft. Instead, we assumed a 750-m field of vision from either side of the aircraft, resulting in a total width of the survey of 1.5 km, on the basis of Rowat et al. (2009). Furthermore, constant altitude and speed were maintained during the aerial surveys to avoid additional biases. A perception correction factor was not applied because all whale sharks should be observable below the altitude of 800 m (Rowat et al., 2009).

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Data analysis

The area surveyed was calculated as the length of the transect multiplied by the defined width of the survey (1.5 km). To standardize abundance data, density of animals by species was calculated for each flight and by month and year, by using the method described by Rowat et al. (2009), with the following formula:

$$A = C / SI,$$

where A = density;
C = counts of whale sharks or giant mantas; and
SI = survey intensity (in square kilometers).

Densities of whale sharks and giant mantas were compared between areas (the WSBR and Azul area), among years, and among months by using a nonparametric Kruskal–Wallis test (P<0.05). Finally, maps of distribution and abundance were generated for each species by using QGIS software, vers. 2.18.26 (QGIS Development Team, 2018).

Results

From 2016 through 2018, 17 aerial surveys were conducted in the WSBR and Azul area. During 28 h of flight, 4571 km were covered along the transect, resulting in a surveyed area of 6857 km^2. A total of 953 whale sharks and 466 giant mantas were seen (Table 1). Occasionally, both species were observed interacting in the same area.

Table 1

Number of whale sharks (*Rhincodon typus*) and giant mantas (*Mobula birostris*) observed during aerial surveys conducted between May and September during 2016–2018 in the northern Caribbean Sea off Mexico. Most surveys were conducted from 0730 to 1130. An asterisk (*) indicates that surveys were conducted in the afternoon from 1500 to 1800.

Date of survey	Surveyed area (km^2)	Number of whale sharks observed	Number of giant mantas observed
26-July-2016	469.5	0	0
27-July-2016	388.5	120	87
25-Aug-2016	486.0	151	0
26-Aug-2016	481.5	121	13
21-Sept-2016	493.5	1	0
22-Sept-2016	415.5	17	125
18-July-2017*	247.5	10	4
20-July-2017	448.5	170	1
12-Aug-2017*	243.0	14	110
13-Aug2017	234.0	56	21
19-Sept-2017	528.0	10	3
20-Sept-2017	384.0	9	3
23-May-2018	363.0	3	36
13-July-2018	472.5	92	31
29-July-2018	367.5	109	7
23-Aug-2018	475.5	68	25
19-Sept-2018	358.5	2	0
Total	6857	953	466

Occurrence of whale sharks

The average number of whale sharks observed per flight was 56 (standard deviation [SD] 59). In July 2017, the largest number of whale sharks counted was 170; these sharks were aggregated in a 3.8-km^2 area. The next 2 largest groups were recorded in August 2016. During the first and second flights in August 2016, 151 and 121 whale sharks were counted, respectively. Overall, the largest aggregations were observed in the Azul area. However, it is most likely that the whale sharks recorded in one month were the same individuals observed in the following month. The largest annual number of sightings of whale sharks was recorded in 2017, with a total of 410 individuals counted, in comparison with 274 and 269 individuals counted in 2018 and 2016, respectively (Fig. 3).

The average density was 14 individuals/100 km^2 (SD 14) during 2016–2018. Although densities of whale sharks recorded in the Azul area were higher than densities in the WSBR, the differences were not statistically significant (Kruskal–Wallis test: P=0.46). Survey results indicate that there were no differences in density of whale sharks among years (Kruskal–Wallis test: P=0.69) (Fig. 4) but that there were significant differences among months (Kruskal–Wallis test: P=0.04). Results from surveys conducted in September indicate a significant decrease in recorded density from levels observed in July and August.

Occurrence of giant mantas

The average number of giant mantas observed per flight was 27 (SD 40). The single largest number of individuals observed during one flight was 125. The largest group was recorded in September 2016, with 120 giant mantas distributed in an area of 1.2 km^2. The second-largest aggregation observed was recorded in August 2017, with 100 giant mantas located north of the Azul area but still in the MCBR. A third group of 80 individuals moving linearly in the Azul area was recorded in July 2016 (Fig. 5).

The largest annual number of giant mantas was recorded in 2016, with a total of 225 individuals counted, a year before the largest annual number of whale sharks was observed. Sightings of 142 and 99 giant mantas were recorded in 2017 and 2018, respectively (Fig. 6). From 2016 through 2018, the average density of giant mantas was 8 individuals/100 km^2 (SD 13). Survey results indicate that there were no differences in density of giant mantas among months (Kruskal–Wallis test: P=0.81), among years (Kruskal–Wallis test: P=0.62), or between areas (Kruskal–Wallis test: P=0.67).

Discussion

The site of aggregation of whale sharks and giant mantas in the northern Caribbean Sea off Mexico covers an area of

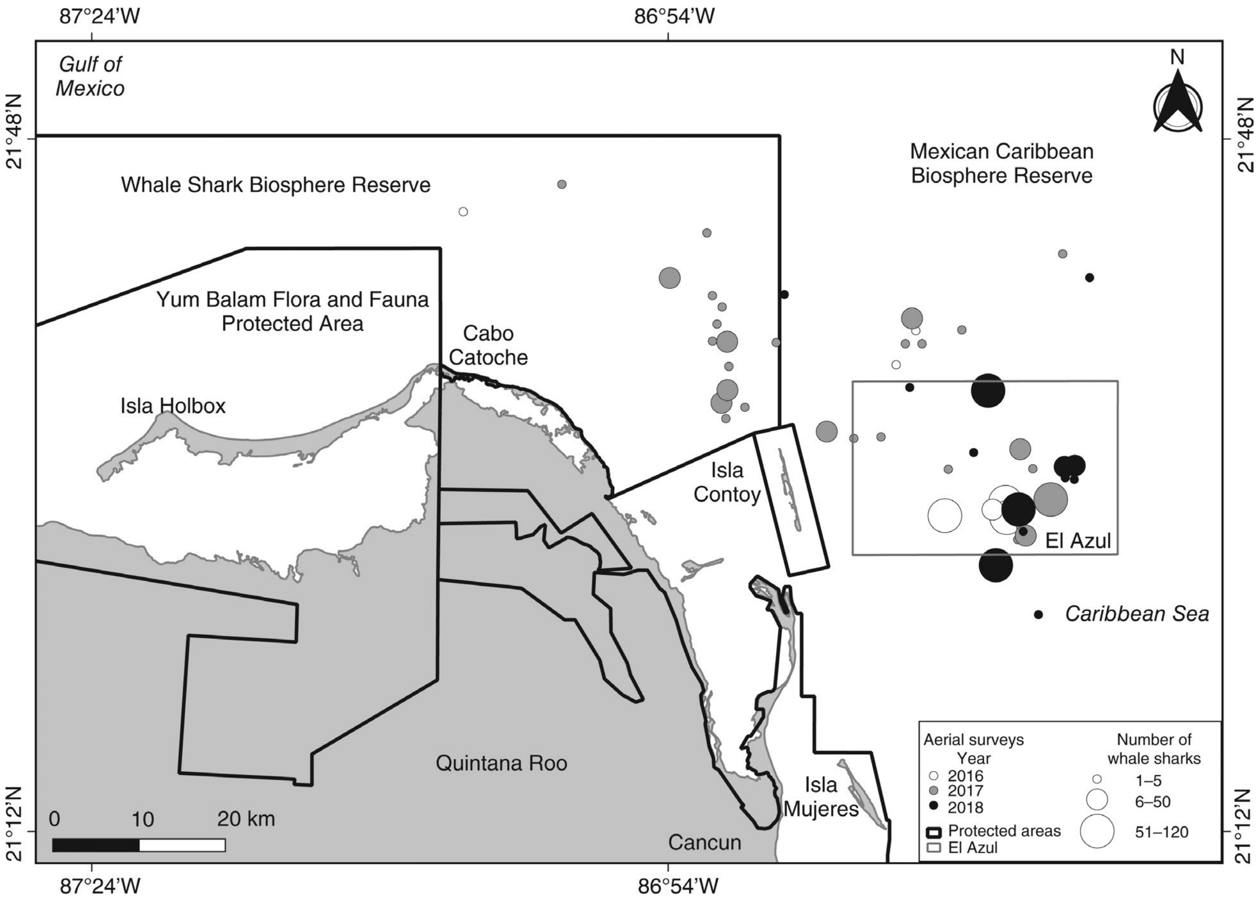

Figure 3

Map showing the distribution and abundance of whale sharks (*Rhincodon typus*) in the northern Caribbean Sea off Mexico based on data obtained from aerial surveys conducted between May and September during 2016–2018. Circle size is proportionate to the number of whale sharks observed, and circle shade corresponds to the year in which the sighting was made. The black and gray lines indicate the boundaries of protected areas and of the Azul area, respectively.

approximately 6334 km^2 (DOF, 2018a). In such large marine areas, aerial surveys facilitate surveys of the abundance of whale sharks and giant mantas by reducing the time spent on monitoring activities. In this study, we spent an average of 165 min on flight time per transect. A survey of the same transect by boat could take an estimated time of 9 h.

Prior to our study, aerial surveys have been used successfully to describe distribution and abundance of marine megafauna, such as marine mammals, manta rays, and whale sharks (Gifford et al., 2007; Rowat et al., 2009; Salberg et al., 2009; Laidre and Heide-Jørgensen, 2011). During most of the aerial surveys conducted (94%), whale sharks and giant mantas were sighted. However, a limitation of aerial surveys in monitoring of marine megafauna is not being able to detect animals at depths >3 m. Nevertheless, aerial surveys are useful for assessing the distribution and abundance of whale sharks and giant mantas because of the time that these animals spend near the sea surface. Also, aerial surveys could help with estimation of the size of aggregations and even with collection of information about tourist activities (e.g., number of boats present).

Another restriction of aerial surveys in monitoring marine megafauna is the limited time available to observe the same point on a transect. Previous studies have determined that whale sharks move between the WSBR and Azul area (Hueter et al., 2013). The use of aerial surveys is a more appropriate technique for assessing abundance of whale sharks because it is easier to observe different groups throughout a survey area and reduce the error of counting the same individual more than once.

Occurrence of whale sharks

Most sightings of whale sharks were recorded in the Azul area, which since 2009 has been reported to have the highest abundance of this species (Cárdenas-Palomo et al.,

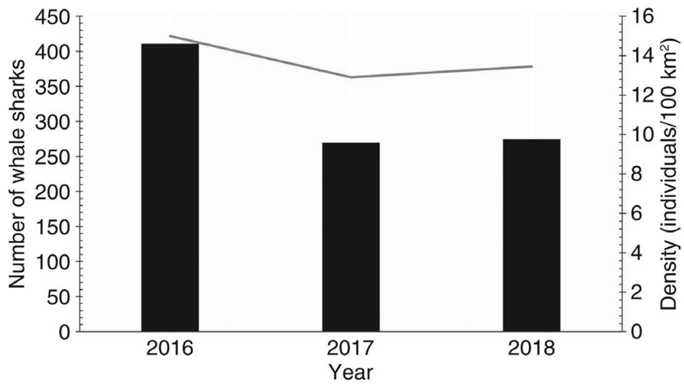

Figure 4

Number of whale sharks (*Rhincodon typus*) recorded during aerial surveys conducted in the northern Caribbean Sea off Mexico between May and September in 2016–2018. The gray line indicates estimates of density of whale sharks based on data from these surveys.

2015; Cárdenas-Palomo et al.[2]). During this study, only 7 groups of more than 70 whale sharks each were observed, all in the Azul area. Despite the importance of this area for whale sharks, it did not become a protected area until 2016, when the MCBR was established.

The Azul area is extensive, with an area of approximately 400 km^2, and it is commonly difficult to move through it by boat at a speed greater than 40 km/h because of sea conditions. As a result, aerial surveys are more efficient than boat censuses because locations of whale sharks can be identified in less time and counts of individuals are more accurate.

In the Caribbean Sea off Mexico, as in many other sites of aggregation of whale sharks around the world, the relationship between abundance and food availability has been identified (Sequeira et al., 2012; Cárdenas-Palomo et al., 2015; Pierce and Norman, 2016). The average zooplankton biomass in the Azul area during the spawning period of the little tunny (*Euthynnus alletteratus*) has been recorded at values >4000 mg/m^3, much higher than the maximum value recorded in the WSBR (approximately 600 mg/m^3). This difference in zooplankton biomass is perhaps the reason that whale sharks prefer to aggregate in the Azul area when fish are spawning (de la Parra Venegas et al., 2011; Cárdenas-Palomo et al.[2]). In our study, whale sharks inside the WSBR were observed only in July 2017. Possibly, at that time, the amount of food available in surface layers in the WSBR had increased as a result of upwelling pulses that raised productivity.

In a previous study conducted in the Azul area during 2005–2009, the reported average number of sightings of whale sharks was 67.5 individuals/flight (de la Parra Venegas et al., 2011). The kind of aircraft used and months in which the monitoring was carried out in that study were the same as those in ours. In our study, an average of 56 individuals/flight were recorded, which is 17% lower than the number of individuals observed during 2005–2009 in the previous study. A declining trend in abundance of whale sharks has already been reported for the Caribbean Sea off Mexico (Cárdenas-Palomo et al.[2]) and for other aggregation sites around the world (Rowat and Brooks, 2012; Rohner et al., 2013; Norman et al., 2017). According to Rohner et al. (2013), it is possible that broad-scale oceanographic variables could be driving the decrease in sightings of whale sharks or that the apparent decrease could be attributed to a genuine population decline. To address these unknowns for the aggregation of whale sharks in the Caribbean Sea off the Yucatan Peninsula, additional research of other ecosystem components, such as direction and intensity of ocean currents, is needed, as is information related to the population ecology and biology of this species.

From 1999 through 2015, 1115 individuals have been identified by using photographs taken in and above the Caribbean Sea off Mexico. Considering that the estimated population size for whale sharks in the western Atlantic Ocean is 2167 individuals (McKinney et al., 2017), the aggregation site in the Caribbean Sea off Mexico is a hotspot for this species (Hueter et al., 2013; Norman et al., 2017). Our knowledge about whale sharks has increased in recent years. However, it is also important to understand threats to habitat that could influence changes in distribution or abundance of this species (e.g., changes in fish spawning, global warming, and possible effects of tourist activities).

Occurrence of giant mantas

Except in 2018, most of the sightings of giant mantas were recorded north of and inside of the Azul area. These results are not consistent with those of previous studies carried out in the region during 2007–2011 (Hinojosa-Álvarez, 2009; Martínez Urrea, 2015). During these studies, areas within the WSBR, one located north of Cabo Catoche, the northernmost point of the Yucatan Peninsula, and another located northwest of Isla Contoy, were identified as the most important sites for this species. The shifts between feeding zones through time could be determined by zooplankton abundance, composition, or spatial availability. Large elasmobranch species seem to prefer sites where zooplankton are abundant, a preference that may be related to the amount of energy

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[2] Cárdenas-Palomo, N., J. Trujillo-Córdova, E. Mimila-Herrera, J. Herrera-Silveira, J. I. Velazquez-Abunader, I. Osorio, and O. Reyes-Mendoza. 2020. El hábitat del tiburón ballena. *In* Tiburón ballena en el Caribe Mexicano: acciones para su conocimiento y conservación, p. 31–48. Technical report Project “Manejo sustentable del tiburón ballena en el Caribe Mexicano” conducted by Pronatura Península de Yucatán A.C., CINVESTAV-IPN Unidad Mérida, with the support of World Wildlife Fund and Carlos Slim Foundation. [Available from Pronatura Península de Yucatán A.C., Calle 32 No. 269, Pinzon II, 97205 Merida, Yucatan, Mexico.]

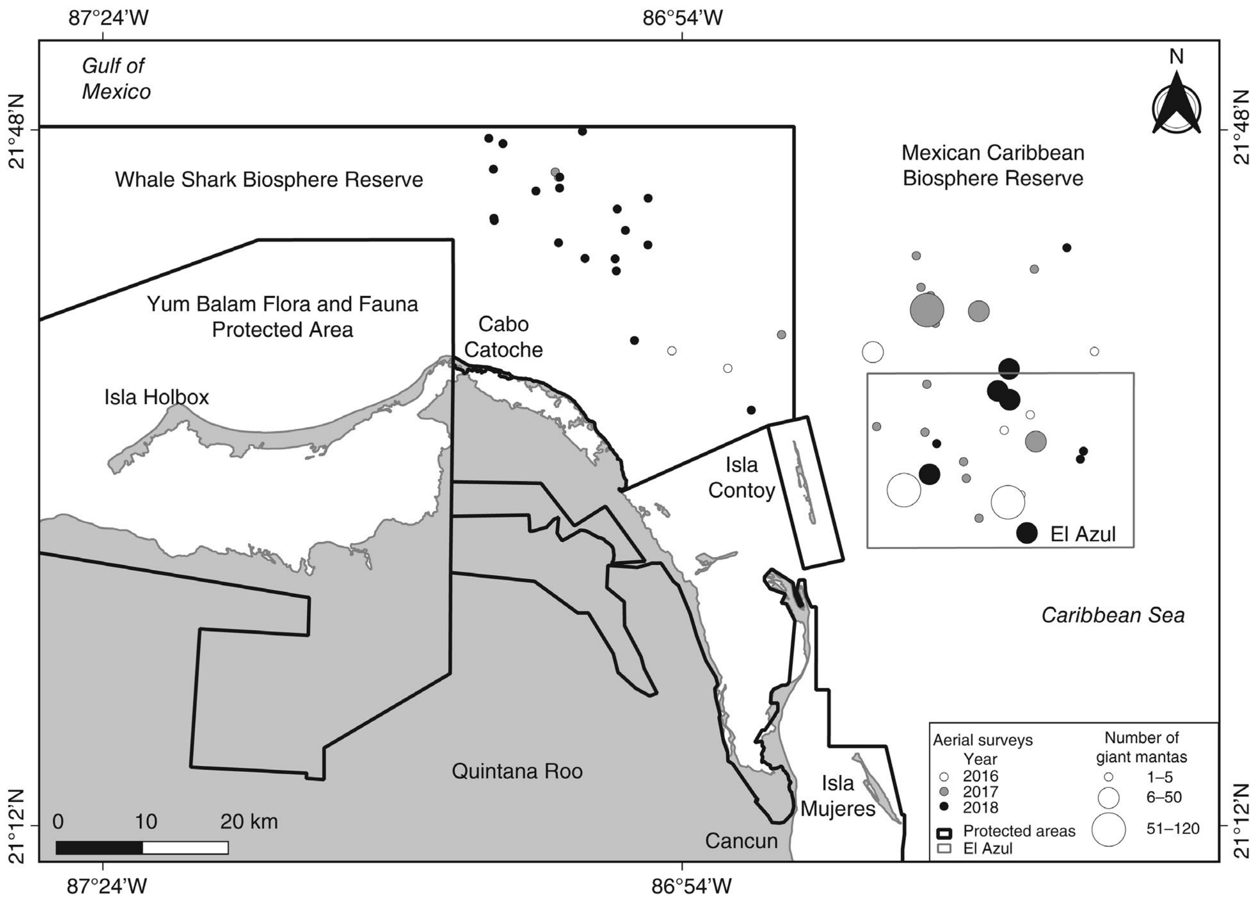

Figure 5

Map showing the distribution and abundance of giant mantas (*Mobula birostris*) in the northern Caribbean Sea off Mexico based on data obtained from aerial surveys conducted between May and September during 2016–2018. Circle size is proportionate to the number of giant mantas observed, and circle shade corresponds to the year in which the observation was made. The black and gray lines indicate the boundaries of protected areas and of the Azul area, respectively.

spent to locate, capture, and consume those prey (Nelson and Eckert, 2007).

It should be noted that the zone where giant mantas aggregate in the Caribbean Sea off Mexico has already been identified as a feeding site (Graham et al., 2012; Hacohen-Domené et al., 2017). By tracking movements of animals with satellite tags inside of the Azul area, Graham et al. (2012) described feeding areas of giant mantas in the locations where the largest aggregations were recorded in this study.

Reef manta rays (*Mobula alfredi*) form large aggregations (>30 individuals); in comparison, giant mantas are seldom encountered in such numbers. The overall global population sizes of both species are unknown, but subpopulations appear, in most cases, to be less than 1000 individuals (Marshall et al., 2018). During the 3 years of this study, 3 large groups of giant mantas (>80 individuals) were recorded; the largest group, of at least 120 individuals, was observed in 2016. Hinojosa-Alvarez (unpubl. data, 2010; as cited by Marshall et al., 2018) estimated the size of the subpopulation of giant mantas in the Caribbean Sea near Holbox Island, off the northeastern coast of the Yucatan Peninsula, at around 100 individuals. Our results indicate that this number is underestimated and may not represent the real size of the subpopulation in this area.

Martínez Urrea (2015) reported approximately 300 giant mantas in the Azul area during 2009. However, because the author did not provide a relative abundance index, we cannot determine whether there was an increase or decrease in sightings of giant mantas between 2009 and the years of our study. Nevertheless, it has been estimated that there has been at least a 30% decrease in the worldwide population of giant mantas over the last 75 years or so (Marshall et al., 2018). Efficient conservation strategies, therefore, are required to protect areas, such as the northern Caribbean Sea off Mexico, that have a high density of giant mantas.

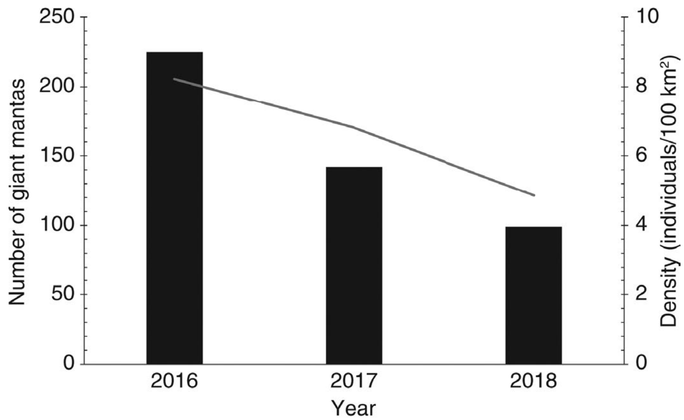

Figure 6

Number of giant mantas (*Mobula birostris*) recorded during aerial surveys conducted in the northern Caribbean Sea off Mexico between May and September in 2016–2018. The gray line indicates estimates of density of giant mantas based on data from these surveys.

Shared aggregation areas

Frequently, we observed aggregations of whale sharks and giant mantas sharing the same area, indicating that both species share resources in the Caribbean Sea off the northeastern coast of the Yucatan Peninsula. Although foraging strategy theory includes the notion that species partition resources to avoid competition (Hinojosa-Álvarez, 2009; Motta et al., 2010), recent data indicate that a dietary overlap exists between both of these planktotrophic elasmobranch species. Results from a trophic ecology study, based on an analysis of skin samples obtained from whale sharks and giant mantas from the northern Caribbean Sea off Mexico in 2010–2012, provide evidence of an alternative hypothesis of dietary overlap between these elasmobranch species (Hacohen-Domené et al.[3]). Additionally, Couturier et al. (2013) reported similar dietary preferences between whale sharks and reef manta rays in Mozambique, on the basis of comparisons of fatty acid profiles of skin samples.

Understanding the factors that affect and allow the coexistence of both planktotrophic elasmobranch species is important. Inside the WSBR, the abundance of zooplankton is a consequence of the Yucatan upwelling system. As a highly productive ecosystem, food resources might not be limited in this zone from May through September. However, the Azul area is the most important aggregation area for whale sharks and giant mantas because the quantity of available food there is much higher than in the WSBR, and it is concentrated in small patches, resulting in lower energy costs for species during foraging (Nelson and Eckert, 2007; Motta et al., 2010). In another area north of the Azul area, giant mantas were observed almost exclusively, and a high abundance of this species was observed. This area could be critical habitat for giant mantas, a place where they can forage and avoid competition. To our knowledge, there is no published information about zooplankton in this area.

Diverse economic activities, both extractive and non-extractive, are conducted in the Azul area. These activities produce a high frequency of marine traffic, such as that of cargo ships, tourist cruises, and fishing vessels, as well as that of tour boats that provide viewing of and diving near whale sharks (Graham et al., 2012; DOF, 2018b). Although these activities provide economic benefits to nearby communities, they represent a threat to whale sharks and giant mantas. This harm is evident in the high frequency of injuries by propeller impacts (especially for whale sharks; Pierce and Norman, 2016; Marshall et al., 2018). Other threats to giant mantas are from directed take and bycatch (Graham et al., 2012). Therefore, in the short term, delimiting important sites where these species may be vulnerable can help prioritize protection efforts.

The results of our study contribute to the knowledge of the distribution and abundance of whale sharks and giant mantas. The utility and effectiveness of aerial surveys in monitoring the presence and movements of these species in areas far from a coast have been proven. The distribution and abundance of whale sharks and giant mantas in the northern Caribbean Sea off Mexico indicate spatiotemporal variability, a situation that many times has obstructed the implementation of suitable management strategies for their conservation. Long-term data sets are key for assessing abundance trends of these endangered and mobile species. Because it is one of the few areas where whale sharks and giant mantas coincide in time and space, the northern Caribbean Sea off Mexico is an important location for future research.

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