

Dancing with the devil: courtship behaviour, mating evidences and population structure of the *Mobula tarapacana* (Myliobatiformes: Mobulidae) in a remote archipelago in the Equatorial Mid-Atlantic Ocean



Correspondence:
Sibele Alves de Mendonça
sibele_mendonca@yahoo.com.br

Sibele Alves de Mendonça^{1,2} Bruno César Luz Macena^{1,3}, Camila Brasilino Botêlho de Araújo¹, Natalia Priscila Alves Bezerra¹ and Fabio Hissa Vieira Hazin^{1,2}

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The present work aimed at studying the sicklefin devil ray (*Mobula tarapacana*) that aggregates seasonally in the Saint Peter and Saint Paul Archipelago (SPSPA). From December 2008 to June 2016, 827 rays were sighted through free diving visual census survey. From the total of the records, it was possible to identify the sex of 361 specimens, in which 215 were females and 146 were males. The disk width ranged from 2.40 m to 3.20 m with mean size of 2.60 m, for both males and females, indicating that the population is composed by sub-adults and adults. Using photo-identification of the pectoral-fins in the ventral side, 11 males and 44 females were identified and compared with each other, but no re-sight was detected. Recent mating scars were observed in males (n= 7) and females (n= 6), as well as courtship and pursuit behaviors, confirming that the SPSPA is an important area of aggregation and mating for *M. tarapacana* in the Atlantic Ocean.

Keywords: Elasmobranch, Photo-identification, Reproduction area, Sexual aggregation.

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¹ Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco-UFRPE, Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, 52.171-030 Recife, PE, Brazil. (SAM) sibele_mendonca@yahoo.com.br (corresponding author); (CBBA) araujocamilab@gmail.com; (NPAB) natalia_pab@hotmail.com; (FHVH) fvhvazin@gmail.com.

² Departamento de Oceanografia, Universidade Federal de Pernambuco-UFPE, Av. da Arquitetura, s/n, Cidade Universitária, 50740-540 Recife, PE, Brazil.

³ Centro Okeanos, Departamento de Oceanografia e Pescas, Universidade dos Açores- UAç, R. Prof Dr. Frederico Machado, s/n, 9900-138 Horta, Portugal. (BCLM) brunomacena@hotmail.com.

O presente trabalho teve como objetivo conhecer a população da raia manta chilena (*Mobula tarapacana*) que forma agregações sazonais no Arquipélago de São Pedro e São Paulo (ASPSP). Durante o período de dezembro de 2008 a junho de 2016, foram avistadas 827 raias através de censo visual por mergulho livre. Do total das raias avistadas, foi possível identificar o sexo de 361 espécimes, dos quais 215 eram fêmeas e 146 eram machos. A largura de disco variou de 2,40 m a 3,20 m, com média de 2,60 m, tanto para machos como para fêmeas, evidenciando que a população é composta por adultos e sub-adultos. Com base na foto-identificação do padrão de coloração do contorno localizado na região ventral, foram identificados e comparados entre si, 11 machos e 44 fêmeas, não tendo sido observada, porém, nenhuma reavistagem. Marcas de cópula recente foram observadas tanto em machos (n= 7) como em fêmeas (n= 6). Comportamentos de corte e perseguição também foram observados, indicando que o ASPSP é uma importante área de agregação e acasalamento da espécie no Oceano Atlântico.

Palavras-chave: Agregação sexual, Área de reprodução, Elasmobrânquio, Foto-identificação.

INTRODUCTION

A significant increase in catches of Mobulids worldwide due to the growing consumption of gill plates in the Asian market prompted population declines in recent years (Heinrichs *et al.*, 2011; Couturier *et al.*, 2012; Croll *et al.*, 2016; O'Malley *et al.*, 2017). In addition to overfishing, the lack of knowledge on the ecology and population dynamics of devil rays led the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to include all taxonomic group in the Appendix II (CITES, 2017). The International Union for the Conservation of Nature (IUCN), in turn, listed the all devil rays species in different levels of threat (IUCN, 2019), placing the sicklefin devil ray *Mobula tarapacana* (Phillipi, 1892) as “endangered” (Marshall *et al.*, 2019).

The sicklefin devil ray is morphologically characterized by having the pelvic region longer and the spiracle longitudinally elongated (Notarbartolo-di-Sciara, 1988). They have a long head and reduced cephalic fins; a short tail, dorsal coloration ranging from dark brown to olive green and the ventral side white, with a grey posterior border and an irregular but well-marked demarcation line (Notarbartolo-di-Sciara, 1987).

A cosmopolitan species distributed in temperate, subtropical and tropical waters of the Atlantic, Pacific and Indian Oceans, the sicklefin devil ray is more commonly observed in the oceanic environment, although it is also found in the neritic zone (Compagno, Last, 1999; Couturier *et al.*, 2012). Due to its mainly oceanic habit and migratory behavior, travelling great distances in few months (Thorrold *et al.*, 2014), studies about its population dynamics and ecology are difficult and, consequently, still scarce. Such a migratory behavior adds complexity to the planning of spatial management of the species, given the capacity to cross geopolitical borders.

Therefore, despite its wide distribution, the knowledge on *M. tarapacana* life history is still rare; for example, the largest specimen ever observed was a 3.70 m disc width (DW) female (White *et al.*, 2018), and the estimated size at first sexual maturation is 2.50 m and 2.70–2.80 DW for males and females, respectively, with the size at birth between 1.05 and 1.39 m DW (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006; Rambahiniarison *et al.*, 2018). In addition, the biological and ecological information are restricted to a few locations of known aggregations in the world (Couturier *et al.*, 2012; Croll *et al.*, 2016; Pardo *et al.*, 2016), such as Coco's Islands (Costa Rica), in the Pacific Ocean (White *et al.*, 2015); Indonesia, in the Indian Ocean (White *et al.*, 2006); and the Azores (Portugal), in the Northeast Atlantic Ocean (Sobral, Afonso, 2014). In Brazilian waters, the Saint Peter and Saint Paul Archipelago (SPSPA) is the only aggregation site of the species known to date (Mendonça *et al.*, 2018), however, occurrences have been recorded both in the north and northeast coasts, mainly in oceanic islands and seamounts, with a few sightings also reported for the southeastern region (Amorim *et al.*, 2002; Gadig, Sampaio, 2002).

Observations of behavior *in situ* and the identification of animals by natural marks has been successfully used in elasmobranchs (Corcoran, Gruber, 1999; Yano *et al.*, 1999; Castro, Rosa, 2005; Marshall, Bennett, 2010), allowing the estimation of local population parameters, such as size distribution and reproductive aspects, crucial for conservation efforts. Courtship behavior in a natural environment has been observed previously for *M. tarapacana* in the Azores (Sobral, 2013) and for *M. alfredi* (Krefft, 1868) and *M. birostris* (Walbaum, 1792) (Yano *et al.*, 1999; Marshall, Bennett, 2010; Deakos, 2012; Stevens *et al.*, 2018), *M. mobular* (Bonnaterre, 1788) (Duffy, Tindale, 2018), and *M. thurstoni* (Lloyd, 1908) (McCallister *et al.*, 2020). For *M. birostris* and *M. alfredi*, on the other hand, the unique pattern of spots in their ventral region was used to elucidate the population aspects of these species (Luiz Jr *et al.*, 2009; Marshall, Bennett, 2010; Marshall *et al.*, 2011; Deakos *et al.*, 2011; Deakos, 2012; Couturier *et al.*, 2014).

This study aims at providing evidences of reproductive behavior and at describing the population structure of the of *M. tarapacana* in a remote Brazilian oceanic archipelago, using non-lethal methods, such as direct observation and video/photo-identification.

MATERIAL AND METHODS

Study area. The SPSPA is a small group of rocky islets, located in the equatorial part of the Mid-Atlantic Ridge (00°55'02"N, 29°20'42"W) (Fig. 1), about 1,000 km away from Brazil and 1,800 km from Guinea Bissau. The archipelago is under the direct influence of the South Equatorial Current, which flows superficially in the East-West direction, and of the Equatorial Undercurrent, which flows in the opposite direction (W-E), between 60 and 100 m depth (Stramma, England, 1999). The interaction of these currents with local topography causes turbulent processes typically observed in seamounts, such as vortexes, stream velocity reductions, thermohaline structure disturbances and local resurgence mechanisms that result in scattered enrichment of surface waters (Araujo, Cintra, 2009).

Due to the particular oceanographic conditions of the SPSPA, from January to June,

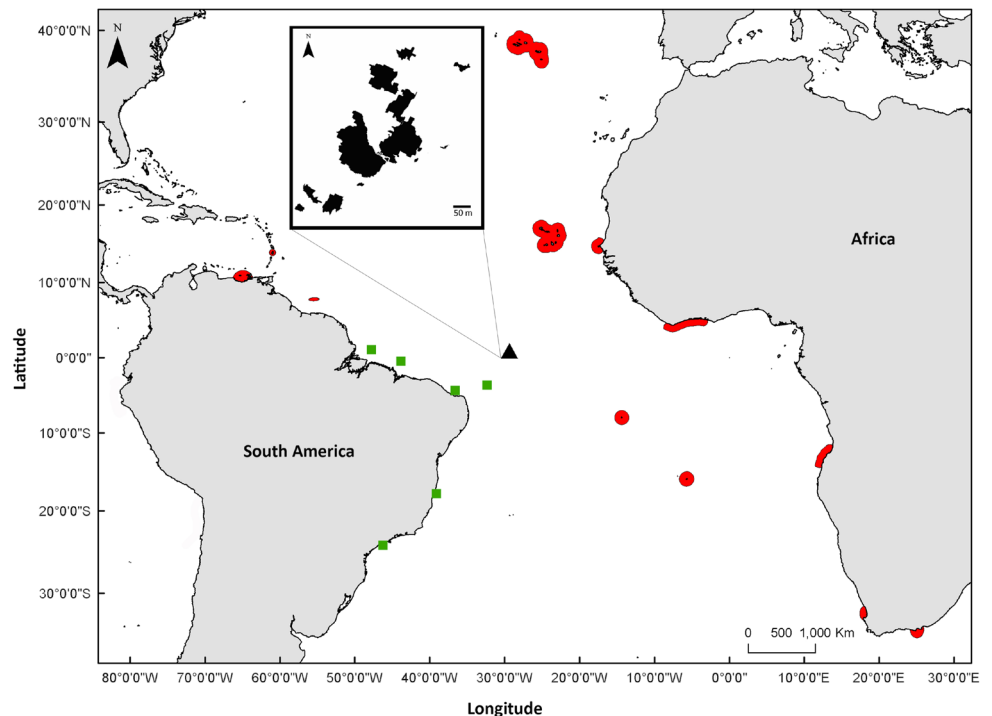


FIGURE 1 | Geographical location of the Saint Peter and Saint Paul Archipelago (SPSPA; black triangle and inset) in the equatorial Atlantic Ocean. Red indicates *Mobula tarapacana* confirmed occurrences in the Atlantic Ocean (IUCN, 2019), while green squares are known occurrences in Brazilian waters.

the water is enriched with zooplankton, eggs and larvae of fishes and invertebrates (Macedo-Soares *et al.*, 2012), providing a suitable habitat in the oceanic domain for filter-feeding species, in particular the whale shark *Rhincodon typus* Smith, 1828 (Macena, Hazin, 2016) and the devil rays, which aggregate seasonally, during this period (Mendonça *et al.*, 2012; 2018; Hazin *et al.*, 2018).

Data collection. Between December 2008 and June 2016, 38 expeditions to SPSPA, of 15 days each (570 d), were undertaken, with the majority of expeditions (76%) occurring in the first half of the year, the period of greatest abundance of the species in the region (Mendonça *et al.*, 2018). Observations of the devil rays were done through free diving mainly on the west side of the islands (Fig. 1). Due to logistic restrictions, the surveys were done in association with the fishermen schedule; restricted mainly from 7 am to 1 pm. The diving time, presence/ absence of rays, and the time and period they stayed in sight were then recorded. Whenever the rays approached the divers, photographs and/or videos were made, to identify the gender and to record behavior. The DW was estimated either by comparison to the pole used for tagging (Mendonça *et al.*, 2018) or with an object/ diver of known size. In order to assess the maturity stage of the population a proxy of 2.7 m and 2.5 m was used for females and males, respectively, according to the information available (White *et al.*, 2006; Rambahiniarison *et al.*, 2018). The image database included all records (videos and photos) with date, sex, size and behavior observed; and was

also used for photo-identification. *Mobula tarapacana* have a unique ventral pattern forming greyish undulations that allow the identification of individuals (Sobral, 2013; Mendonça, 2018). The ventral pictures were compared visually, with the ventral pattern of coloration being analyzed in detail. Other pictures of the dorsal region and additional marks, such as scars or bite injuries, that could help to distinguish the individuals were also looked for. However, how long these marks on the dorsal region remain over the years, after the healing period, is not known.

We also observed evidences of copulation marks on the pectoral fins of females and abrasion at the tip of the clasper and a swollen pelvic region, in males (Fig. 2) (Marshall, Bennett, 2010). The complex mating process described for both manta rays species as sequence of chasing, biting, copulating, post-copulation holding and separation (Yano *et al.*, 1999, Stevens *et al.*, 2018) was compared to the behavior observed in the present study. The devil rays were considered to be swimming in a group when two or more specimens were sighted at the same occasion.



FIGURE 2 | Spot patterns used for photo identification of *Mobula tarapacana* in the Saint Peter and Saint Paul Archipelago (SPSPA).

Data analysis. The Kolmogorov–Smirnov test was performed with the objective of assessing the differences between the size (DW) of males and females (Sokal, Rohlf, 1995). Since the DW was visually estimated, we conservatively expect an error estimate of ± 0.5 m thus generated a new dataset (resample) including the bias (± 0.05 m intervals randomly added to the sizes), following Macena, Hazin (2016). We generated (bootstrapped) 10,000 different datasets with the random bias, statistically compared each mean of the surveyed DW dataset with resampled DW dataset using Student t-test and verified the proportion of the t-test p-values (< 0.05) within the 95% of confidence interval to validate the surveyed visual size estimation. The statistical test was performed in R programming with 0.05 significance level.

RESULTS

Eight hundred and twenty-seven sightings of *M. tarapacana* were recorded from December 2008 to June 2016. Sex could be identified 361 times (43.6%), with females being more frequent (215; 59.6%) than males (146; 40.4%), resulting in a sex ratio of 1.47: 1.00, respectively. It is not possible, however, from these data, to ascertain whether a same specimen has not been counted twice. Considering only those specimens uniquely identified by the pattern of coloration in the posterior ventral region (Fig. 2), it was possible to identify the sex of 55 individuals, 44 of which were female and 11 males, resulting thus in a sex ratio more strongly biased towards females (4: 1). The great number of non-identified sex ($n = 466$) was related to the sea conditions (e.g. big swell, water clarity and high current speed), swimming depth and distance of the rays, as well as to the short time during interactions. Additional difficulties were the large number of rays when in groups and the small size of male claspers in individuals close to or less than 2.50 m DW.

Some *M. tarapacana* (15 females and nine males) also presented scars of bites inflicted by the cookie-cutter shark *Isistius* sp. Gill, 1865, usually in the dorsal region, or by other sharks or fish, in the posterior region of the pectoral and pelvic fins. There were no inter-annual re-sighting over the study period of these specimens for this method, though one individual was sighted in 2015 with an external acoustic tag, similar to the ones used in the SPSPA, from 2009 to 2012 (Mendonça *et al.*, 2018), but it was not possible to identify its identification number.

The estimated DW of 179 (22%) rays ranged from 2.00 to 3.20 m, with a mean \pm SD of 2.60 ± 0.19 m for both genders pooled (Fig. 3). The overall DW of males ($n = 65$; 2.60 ± 0.21 m) and females ($n = 114$; 2.60 ± 0.17 m) were not significantly different (Kolmogorov–Smirnov; $p = 0.40$). The bootstrap of DW dataset validate our visual estimates, since 10,000 runs the grand mean was 2.63 (± 0.34) m DW ranging from 2.53 to 2.72 m. No difference was found comparing both means surveyed and resampled, with the confidence interval of 95.13% indicating no difference, since only 4.87% of the p-values were less than 0.05. The bias considered in visual estimate was acceptable thus used for further demographic analysis.

One hundred and eighty-seven groups were observed during the study, ranging from 2 to 24 (mean \pm SD = 4.32 ± 3.56) rays per group. The highest frequency of large groups ($n = 81$) was observed in April and May. Solitary individuals were observed in 161 occasions.

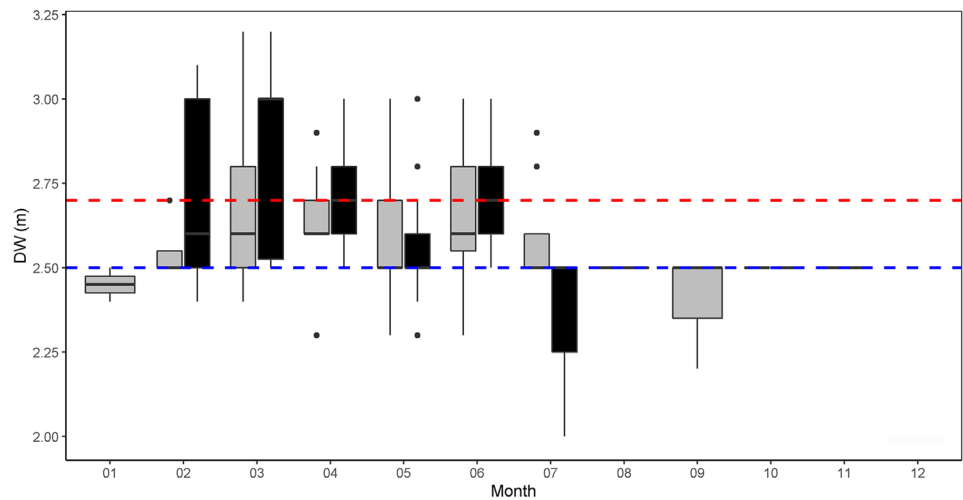


FIGURE 3 | Female (grey) and male (black) *Mobula tarapacana* size distribution (disk width- DW, in meters) per month, in the Saint Peter and Saint Paul Archipelago (SPSPA), from December 2008 to June 2016. Red dashed line= size at maturity for males (White *et al.*, 2006); blue dashed line= size at maturity for females (Notarbartolo di Sciara, 1988).

Recent mating scars or other evidences of mating were observed in both males ($n=7$) and females ($n=6$). In males, abrasions and swollenness/ deformities were observed in the claspers (Figs. 4B, D); while the females had scars in one or in both pectoral fins (Figs. 4A, C). One female also presented a longitudinal scar on the middle back that may have been caused at the time of the chase, when the male makes repeated efforts to grasp her pectoral fin with his mouth, which may suggest a courtship scar. However, further details are needed to understand the courtship' behavior. These potential mating scars were observed in April (2010, 2014 and 2015) and May (2014 and 2015), same months when the largest groups were also seen. In addition to the mating scars, courtship behaviors were observed 14 times, mainly chasing trains, where sometimes the female was chased by one, two or more males (Fig. 5), with the rays swimming randomly in circles and overlapping each other. Males made pelvic movements up and down, during courtship, in circles, apparently preparing for copulation. Observations of chasing trains did not last more than a minute, with the rays moving away quickly. No actual copulation has been observed in the region so far.

Interspecific interactions between *M. tarapacana* and other congeners, such as *M. thurstoni* and *M. birostris*, with the whale shark, and the bottlenose dolphin, *Tursiops truncatus*, were also recorded. In these occasions, *M. tarapacana* was usually following the other animals. Large remoras (*Remora* Gill, 1862) were often observed attached to the *M. tarapacana* body, as well.

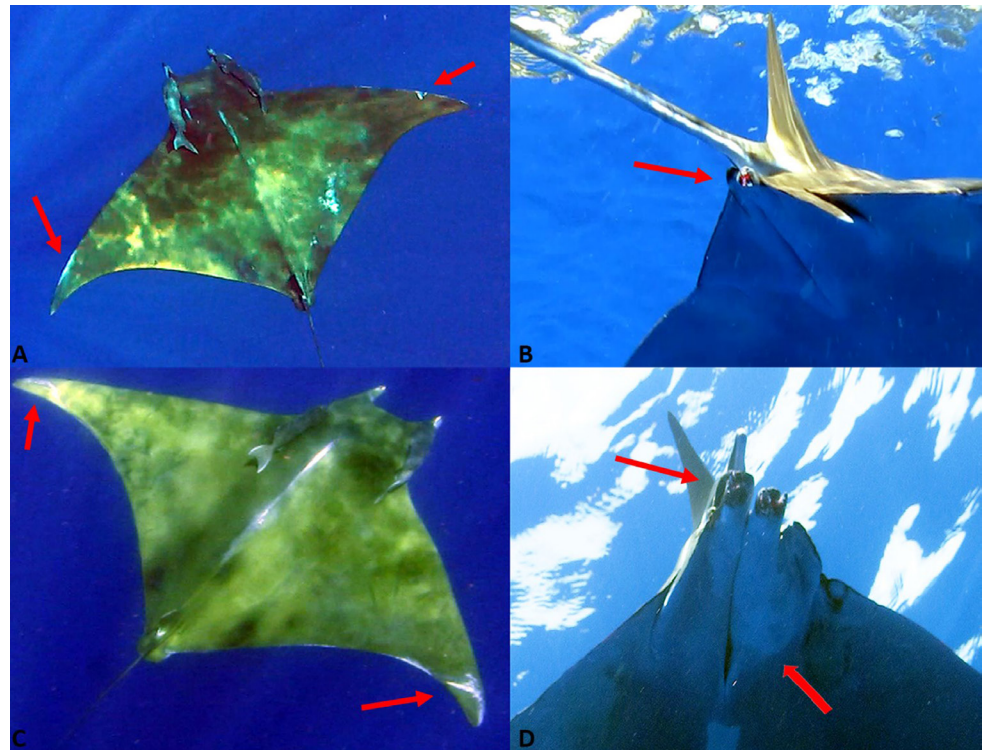


FIGURE 4 | *Mobula tarapacana* observed in the Saint Peter and Saint Paul Archipelago. Left panel- females with evidence of mating scars on pectoral fins. Right panel- males with evidences of mating on the claspers (swollen and/or abraded).

DISCUSSION

The present study suggests that *M. tarapacana* is using the archipelago as a mating ground, due to the evidences of courtship behavior and of potentially recent mating marks and scars showed. Other species of elasmobranches also use the area during part of their reproductive cycle, such as *M. thurstoni* (Mendonça *et al.*, 2012; McCallister *et al.*, 2020), the silky shark (Hazin *et al.*, 2007), and the whale shark (Macena, Hazin, 2016).

The mating process had been previously described in detail for the *M. alfredi* and *M. birostris* (Yano *et al.*, 1999; Marshall, Bennett, 2010; Stevens *et al.*, 2018). The courtship behavior observed for *M. tarapacana* is very similar to the described for manta rays and also for *M. thurstoni* in the SPSPA (McCallister *et al.*, 2020). However, unlike *M. thurstoni* that has been observed in chasing at high speed, performing flips and somersaults, *M. tarapacana* seems to swim more slowly, particularly during the courting pursuit/trains.

Differently from what has been observed for manta rays in Mozambique, Maldives and Hawaii and *M. mobular* in New Zealand, where full-term pregnant females are common in the same area where copulation occurs (Marshall, Bennett, 2010; Deakos, 2012; Stevens *et al.*, 2018), in SPSPA, only *M. thurstoni* pregnant female was recorded (Mendonça *et al.*, 2012). Neither any specimen >2.0 m, indicating that parturition and nursery are not happening in the archipelago. In contrast, in the Azores (Northeastern

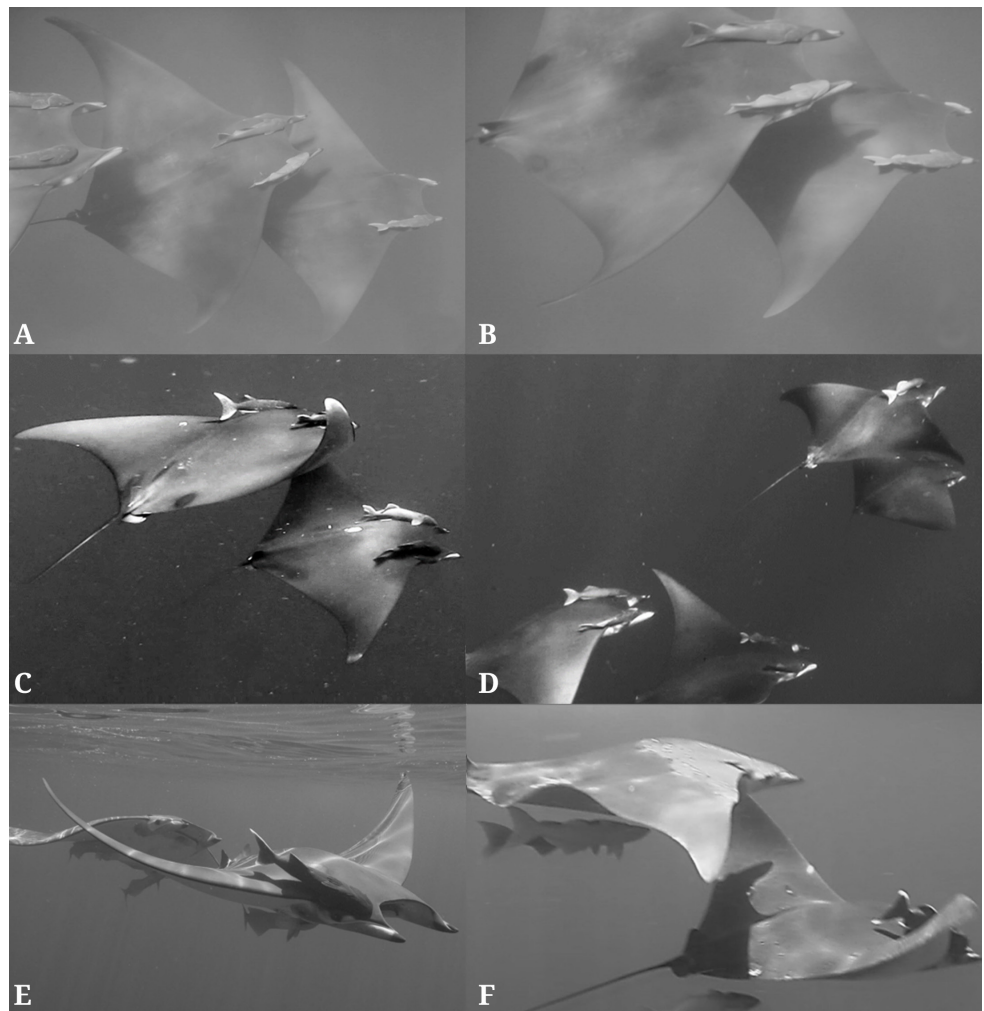


FIGURE 5 | Distinct courtship behaviors of sicklefin devil rays *Mobula tarapacana* observed in the Saint Peter and Saint Paul Archipelago. **A.** Female being chased by two males. **B.** Male overlapping female. **C.** Male trying to overlap on female. **D.** Male overlaps the female with two more males chasing. **E–F.** Sequence of male following female.

Atlantic Ocean), pregnant females of *M. tarapacana* have been observed during August and September (Sobral, 2013).

Despite an overall lack of biological data on *M. tarapacana*, the size at first sexual maturity was calculated as 2.50 m for males (White *et al.*, 2006; Rambahiniarison *et al.*, 2018) and estimated as 2.70 m for females (Notarbartolo-di-Sciara, 1988; Rambahiniarison *et al.*, 2018). Accordingly, most of the *M. tarapacana* observed in the SPSPA were close to the length of their first sexual maturation. The size distribution observed in the SPSPA clearly indicates segregation by size, probably related to reproductive migration as suggested by the mating scars observed in both sexes. The predominance of females, in turn, also suggests the occurrence of a sexual segregation. Sex segregation of mobulid has also been observed previously (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006; Marshall, Bennett, 2010), although this type of behavior might not be so common (Marshall, Bennett, 2010). Notwithstanding, the higher number of females identified in

SPSPA could be merely related to their greater affinity for interaction with researchers, a possibility that requires further investigation.

The lack of re-sighting by photo identification could be resulting either from the relatively low number of individuals identified or due to changes in the spot pattern that might have naturally occurred through time. Nevertheless, one acoustically tagged devil ray was re-sighted during one dive after at least three years of the last deployment season, raising the hypothesis of site fidelity to the SPSPA. In addition, one devil ray monitored with acoustic telemetry returned to the archipelago in two subsequent years (Mendonça *et al.*, 2018). Local fidelity was also observed for other elasmobranchs that occur in SPSPA, such as the hammerhead, *Sphyrna lewini* (Griffith, Smith, 1834) (Bezerra *et al.*, 2019), the silky shark (Lana, 2016) and the whale shark (Bruno C. L. Macena, 2018, pers. comm.).

Despite the broad distribution of *M. tarapacana* on the three ocean basins, aggregation sites are scattered worldwide (Pardo *et al.*, 2016). The SPSPA is an aggregation site for the *M. tarapacana*, which are present there year-round, although their abundance is much higher from January to June, likely to be attracted by the increased availability of food (Mendonça *et al.*, 2018). Congeners such as *M. thurstoni*, *M. mobular* and *M. birostris* also visit the SPSPA (Mendonça *et al.*, 2012; Vaske Jr. *et al.*, 2005; Hazin *et al.*, 2018), highlighting the relevance of the archipelago to the mobulids. The recent mating scars observed in the SPSPA between April and May in three different years reinforces the hypothesis that it has an important role in the migratory and reproductive cycle of the species. Considering this is an oceanic species that inhabits oligotrophic waters, reproductive activities are likely linked to food availability and higher temperatures (Hunter, Goldberg, 1980; Hunter, Macewicz, 1985; Branco, 2011; Bezerra *et al.*, 2013), such as in the case of the ASPSP, during the warmer season, in the first half of the year.

The present study helped to fill the gap on the ecology of the species by providing novel information on population structure and reproductive behavior of *M. tarapacana* thus suggesting that the SPSPA as might be a region in the western equatorial Atlantic for mating, being, therefore, a key area for the conservation of the species.

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AUTHOR'S CONTRIBUTION

Sibele Alves de Mendonça: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing—original draft, Writing—review & editing.

Bruno César Luz Macena: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Writing—review & editing.

Camila Brasilino Botelho de Araújo: Data curation, Formal analysis, Investigation, Methodology, Resources, Writing—review & editing.

Natalia Priscila Alves Bezerra: Data curation, Formal analysis, Investigation, Methodology, Resources, Writing-review & editing.

Fabio Hissa Vieira Hazin: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing-review & editing.

ETHICAL STATEMENT

The methods and data used in this research were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) of the Brazilian Ministry of the Environment n° 50119-1

COMPETING INTERESTS

The authors declare no competing interests.

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