



Spatiotemporal abundance of the whitespotted eagle ray and the giant manta ray (Chondrichthyes: Myliobatiformes) from aerial surveys in southeast Florida

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Abstract This study employed aerial surveys to quantify the spatial and temporal abundance of the whitespotted eagle ray, *Aetobatus narinari*, and the giant manta ray, *Mobula birostris*, in southeast Florida. *Aetobatus narinari* abundance did not differ along the north-south axis of the coast, whereas *M. birostris* was more abundant at lower latitudes. Similarly, *A. narinari* did not exhibit any seasonal difference in abundance, whereas *M. birostris* was more abundant during December and February. Neither species exhibited a clear trend in abundance over the study period (2014–2021). In addition, the abundance of both species failed to correlate with water temperature, chlorophyll-a concentration, or photoperiod. Both *M. birostris* and *A. narinari* are protected species in Florida state waters, and *M. birostris* is designated as threatened under the US Endangered Species Act. In addition, both species are classified by the IUCN as endangered worldwide. Insufficient data exist to establish critical habitat designations for *M. birostris* so that the provided information on their distribution and abundance is useful for the development of effective management.

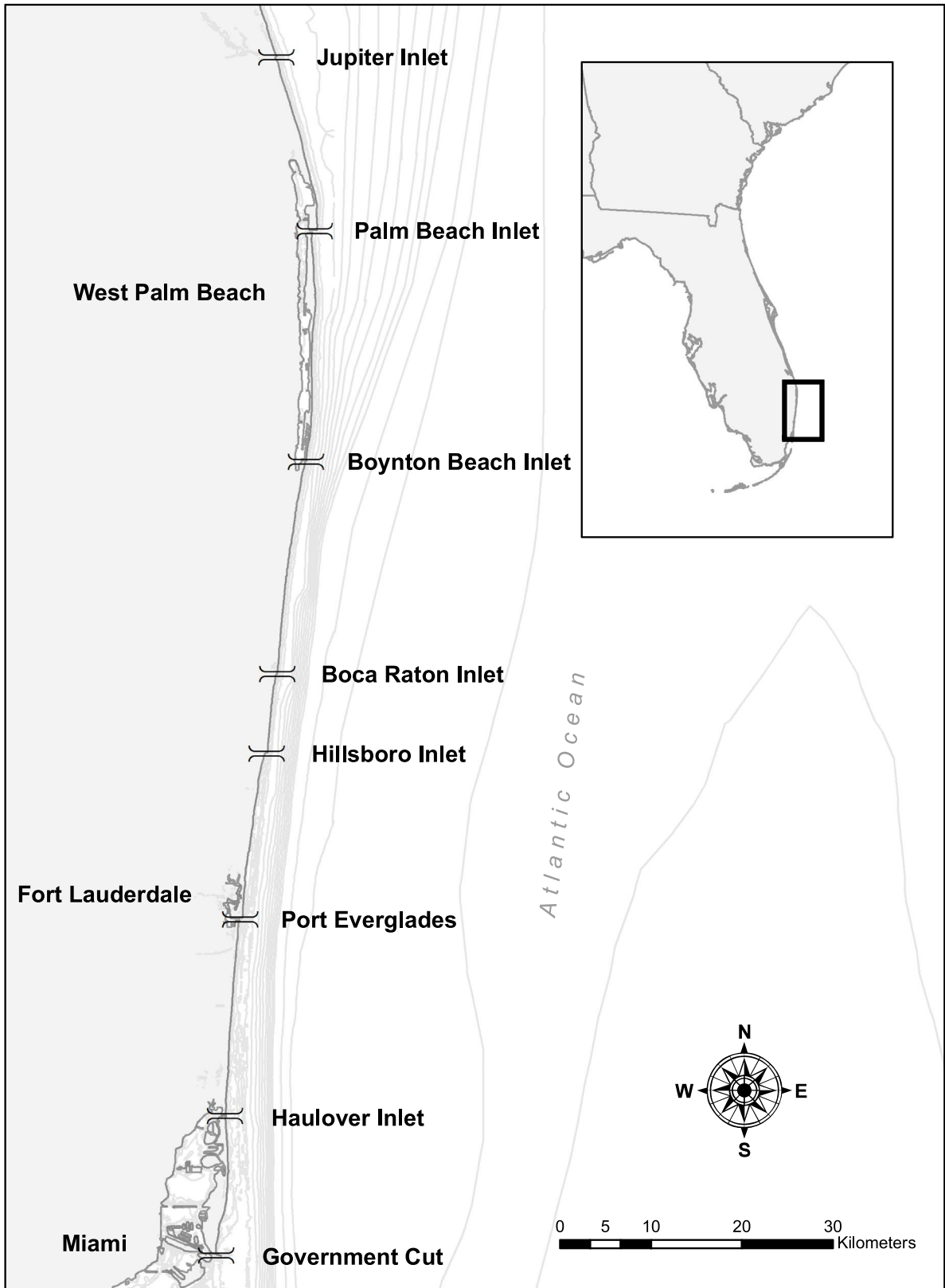
Keywords Aetobatidae · Elasmobranch · Endangered · Mobulidae

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Introduction

Aerial surveys for marine organisms are typically conducted on air-breathing species, such as seabirds (Certain and Bretagnolle 2008), turtles (Lauriano et al. 2011), and marine mammals (Smultea et al. 2014; Edwards et al. 2007), which necessarily come to the surface where they can be seen. However, aerial surveys for marine fishes have also been conducted successfully (Lutcavage et al. 1997; Churnside et al. 2011; Lynn et al. 2014; Bauer et al. 2015). The large body size of many elasmobranch fishes can facilitate visualization from the air (Robbins et al. 2014). Several elasmobranch species have been studied using aerial surveys including sharks (reviewed in Kiszka and Heithaus 2019) and batoids (Clark 1963; Rogers et al. 1990; Blaylock 1993; Girondot et al. 2015; Ajemian and Powers 2016; Armstrong et al. 2020).

Since 2011, an aerial survey has been conducted on a regular basis to quantify the seasonal abundance of sharks along the shoreline of southeast Florida (Kajiura and Tellman 2016). This long term study uses a high-resolution 4K video camera to continuously record the entire survey transect. Analysis of the video footage provides the opportunity to quantify seasonal abundance and spatial distribution of organisms found in the nearshore environment. In addition to the sharks, various other large marine organisms are regularly identified including the West Indian manatee, *Trichechus manatus* Linnaeus, 1758, the



◀**Fig. 1** Map of the study site. Aerial survey flights were conducted along the southeast coast of Florida from Government Cut to Jupiter Inlet. The transect was divided into seven segments demarcated by inlets that were easily visible during review of the video footage.

giant manta ray, *Mobula birostris* (Walbaum, 1792), and the whitespotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790).

The two large batoid elasmobranchs, *M. birostris* and *A. narinari*, are both members of the order Myliobatiformes and share a similar rhomboid body shape with a long, thin tail (Last et al. 2016). Whereas *M. birostris* (family Mobulidae) is characterized by paired cephalic lobes on either side of its terminal mouth, *A. narinari* (family Aetobatidae) is characterized by a distinctly pointed snout that projects anterior to the body (Last et al. 2016). These differences in head morphology, coupled with differences in size and body coloration, serve to distinguish these two species from the air.

Mobula birostris is the largest batoid elasmobranch in the world and can reach up to 7 m in disc width (Last et al. 2016). It has a circumglobal distribution in tropical to warm temperate waters and feeds on planktonic organisms and small bony fishes (Last et al. 2016). Southeast Florida was recently proposed as a nursery area for juvenile *M. birostris*, and individuals are often found in the nearshore environment within 200 m of the beach (Pate and Marshall 2020). The taxonomy of the manta ray species found in the nearshore environment of southeast Florida is under revision and the species currently identified as *M. birostris* might be an undescribed species, *M. cf. birostris* (Farmer et al. 2022). Due to the unresolved taxonomy, this manuscript will use *M. birostris* as the nominal species, with the recognition that the results may eventually apply to the undescribed *M. cf. birostris*.

The other batoid species regularly seen during the aerial survey flights, *A. narinari*, is a benthopelagic ray found in tropical to warm temperate waters in the Western Atlantic (Last et al. 2016; Sales et al. 2019; Brewster et al. 2021). It is a common batoid in nearshore waters of southeast Florida including within lagoons and estuaries (Gilmore 1977; Snelson and Williams 1981; DeGroot et al. 2020). Populations along the Atlantic coast of Florida appear to be largely resident and do not exhibit the migratory

behavior seen in the Gulf of Mexico populations (DeGroot et al. 2021).

Both species are listed as Endangered on the IUCN Red List (Dulvy et al. 2021; Marshall et al. 2022), and *M. birostris* is categorized as threatened under the US Endangered Species Act (NOAA 2018). In Florida state waters, where this study occurred, both species are listed as protected by the Florida Fish and Wildlife Conservation Commission. Given the conservation concerns identified for these species, it is important to gather as much information as possible on the habitat utilized by both species to provide effective management. Therefore, this study used aerial survey footage to quantify seasonal abundance and spatial distribution of these two large batoid species in the nearshore waters of southeast Florida.

Methods

To quantify the abundance and distribution of large batoids in the nearshore environment, an aerial survey was conducted following the methods outlined in a previous study (Kajiura and Tellman 2016). A Cessna 172 aircraft was outfitted with a Sony FDR-AX33 4K video camera mounted on a bespoke aluminum bracket out of the open pilot's side window and aimed downward to capture a field of view from the side of the plane to the shoreline. A polarizing filter was employed to reduce glare off the water surface. The camera recorded continuously along the length of the transect at 30 fps with the shutter speed set to 1/1000 s and the focus set to infinity. Commentary from the pilot throughout the flight was recorded on the audio track and used to provide additional information on animal sightings.

Aerial survey flights were flown at an altitude of approximately 150 m and an airspeed of approximately 140 km h⁻¹. Flights were conducted approximately 200 m seaward of the shoreline. Flights took place between January 2014 and December 2021. Flights were conducted at approximately weekly intervals from December to April each year and at approximately monthly intervals from May to November in 2020 and 2021. Flights were conducted only when seas were relatively calm, which resulted in good visibility with minimal surface distortion. All flights were flown in the morning between

approximately 08:00–11:00 local time to minimize sun glare off the surface of the water.

The survey transect extended from Government Cut Inlet (25°45'50.7"N 80°07'49.0"W) to Jupiter Inlet (26°56'36.6"N 80°04'15.9"W) (Fig. 1). A series of inlets, which were easily identifiable from the video footage, were used to subdivide the transect into smaller sections (Table 1). The distance between each inlet was measured using the measuring tool in Google Earth. Given the approximate width of the transect (200 m) and the length between inlets, it was possible to calculate the sampled area (km²) for each subsection.

The video footage was reviewed manually to quantify the number of rays of each species within each subsection for each flight. Rays were identified as *A. narinari*, *M. birostris*, or unidentified. The same investigator (JMW) examined all the footage to provide consistency. Any questionable sightings were examined by JMW and SMK to reach a consensus as to the species, but if a consensus could not be reached, the ray was considered unidentified. The number of animals within each subsection yielded a density (rays km⁻²) that was used to facilitate comparison among subsections that differed in sampled area.

Environmental data were collected from online sources. Water temperature data were collected from the National Data Buoy Center at the Lake Worth Pier

station (LKWF1), which is located within the transect between Boynton Beach and Palm Beach inlets. Chlorophyll-a data were retrieved from the National Oceanic and Atmospheric Association Environmental Research Division Data Access Program (ERDDAP) server. The minutes of daylight from sunrise to sunset (photoperiod) were collected from the US Naval Observatory.

Statistical analysis

To test whether there were spatiotemporal patterns in the distribution of rays across the surveyed areas, we separately analyzed the number of rays definitively identified as either *A. narinari* or *M. birostris*. First, we tested whether the average abundance of rays counted during each year changed over the survey period using generalized linear mixed models (GLMMs) with negative binomial error distributions. To account for differences in sampling effort during each year, we included total area surveyed as an offset and year of survey as a random effect. Next, we compared the monthly abundances of rays along a latitudinal gradient along the southeast Florida coast for the months of December to April. Because there was limited sampling from May to November, and only in 2020 to 2021 (Table 2), data from those months were excluded from the statistical analysis.

Table 1 The aerial survey transect was divided into subsections to quantify spatial distribution along the coast. Segments were demarcated by inlets, which could be easily seen and identified from the aerial footage.

	Latitude	Longitude	Length (km)	Area (km ²)
NORTH				
Jupiter Inlet	26.94349	-80.07108	19.32	3.864
Palm Beach Inlet	26.77221	-80.03184	25.13	5.026
Boynton Beach Inlet	26.54514	-80.04189	23.37	4.674
Boca Raton Inlet	26.33579	-80.07015	8.61	1.722
Hillsboro Inlet	26.25746	-80.08114	18.35	3.670
Port Everglades	26.09369	-80.10499	21.39	4.278
Haulover Inlet	25.90006	-80.12128	15.14	3.028
Government Cut	25.7640	-80.13027		
SOUTH				
		Total	131.31	26.262

Table 2 Number of aerial survey flights each month and year throughout the study period. Most survey effort was concentrated from Dec to Apr to capture the peak of the blacktip shark migration with approximately monthly flights from May to Nov occurring in only the last 2 years.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2014	2	2	3	4								3
2015	3	5	2	1								2
2016	4	3		2								2
2017	3	4	4	1								4
2018	3	4	5	1								2
2019	3	3	4	3								2
2020	1	4	4	3	1	1	1	1	1	2		3
2021	2		4	3	1		1	1	1	1	1	2
Total	21	25	26	18	2	1	2	2	2	3	1	20

However, the values are still depicted for comparative purposes. The spatial location of each subsection was designated as the latitude occurring at the midway point between the northern and southern inlets that were used to demarcate each of the seven sections that were surveyed (Fig. 1; Table 1). First, we tested whether the abundances of rays differed across latitudes during each of the tested months using Bayesian generalized linear mixed models (BGLMMs). The number of rays counted in each section was used as the response variable, and latitude and month of survey were designated as fully crossed fixed effects. Natural log-transformed subsection area (Table 1) was used as an offset in the models to account for differences in ray counts expected from surveying different sized areas (Zuur et al. 2009). We used Poisson-lognormal error distribution models for both *M. birostris* and *A. narinari* to account for overdispersion in the data (Elston et al. 2001). Finally, we included year of survey as a random effect to account for differences in survey frequencies and annual ray abundances.

To test whether the abundances of *A. narinari* and *M. birostris* were potentially driven by environmental factors, we also tested whether their abundances were correlated with sea surface temperature, daily chlorophyll-a concentration, and photoperiod. For these analyses, we again fit binomial GLMMs with year as a random effect. All statistical analyses were performed in the R statistical programming environment version 4.2.2 (R core Team 2022). All GLMMs were initially run using the package glmmTMB (Brooks et al. 2017), and model assumptions and other diagnostics were checked using the package DHARMA (Hartig 2022). The random effects variance estimates were on the boundary (i.e., there

was a singularity violation) in the analyses of spatiotemporal trends in the abundances of both species, so we used Bayesian generalized linear mixed models (BGLMMs) using the blme package (Chung et al. 2013). The BGLMM applies a weak Wishart prior distribution to generate more accurate estimates of the random effects variances, without changing the estimates of fixed effects. The car (Fox and Weisberg 2019) package was used to run analysis of deviance tests, and the ggeffects (Lüdtke 2018) and ggplot2 (Wickham 2016) packages were used to generate statistical and graphical summaries of model fits.

Results

A total of 120 survey flights were completed between January 2014 and December 2021. Batoid elasmobranchs were seen on 117 (97.5%) flights. Only three flights resulted in no rays being spotted, and two of those flights (Feb 20, 28, 2015) were curtailed flights of only 76.5 km. *Aetobatus narinari* were seen on 94 (78.3%) survey flights, and *M. birostris* were seen on 84 (70.0%) survey flights. Of the 879 total batoids seen in the survey footage, 412 (46.9%) were *A. narinari*, 282 (32.1%) were *M. birostris*, and 183 (20.8%) were unidentified. The number of individuals spotted per flight ranged from 0 to 21 for *A. narinari*, 0 to 17 for *M. birostris*, and 0 to 10 for unidentified. The total number of all batoids combined ranged from 0 to 43 per flight.

Densities ranged from 0 rays km⁻² to a maximum of 4.07 rays km⁻² for *A. narinari* between Boca Raton and Hillsborough Inlets and 2.34 rays km⁻² for *M. birostris* between Port Everglades and

Haulover Inlets. The maximum density for both species exceeded 1.0 rays km^{-2} for all segments.

Spatiotemporal distribution

We tested whether there were any differences in abundance that correlated with latitude, or month for both species. There was not a strong relationship with latitude for *A. narinari* ($\chi^2 = 3.735$, $df = 1$, $p = 0.053$) (Fig. 2a); however, a greater number of *M. birostris* were found at lower latitudes ($\chi^2 = 4.123$, $df = 1$, $p = 0.042$) (Fig. 2b). The abundance of *A. narinari* also did not differ across the months of December to April ($\chi^2 = 2.886$, $df = 1$, $p = 0.577$) (Fig. 3a), but there were greater numbers of *M. birostris* observed in December and February ($\chi^2 = 12.191$, $df = 1$, $p = 0.016$) (Fig. 3b).

We also tested whether there was a difference in abundance among years over the course of the study period, 2014–2021. We found slight increases in abundance (*A. narinari* slope = 0.076 [95% CIs = -0.015 to 0.167], *M. birostris* slope = 0.077 [95% CIs = -0.046 to 0.201]), but these slopes were not clearly distinguishable from the null hypothesis of no change over time for either species (*A. narinari*, $\chi^2 = 2.656$, $df = 1$, $p = 0.103$; *M. birostris*, $\chi^2 = 1.509$, $df = 1$, $p = 0.219$).

Environmental correlates

We examined how the density of both species correlated with three environmental factors: water temperature, chlorophyll-a concentration, and photoperiod. The abundances of *A. narinari* were not strongly influenced by either temperature ($\chi^2 = 0.551$, $df = 1$, $p = 0.458$), chlorophyll-a concentration ($\chi^2 = 0.001$, $df = 1$, $p = 0.978$), or photoperiod ($\chi^2 = 0.074$, $df = 1$, $p = 0.786$) from December to April (Fig. 3a). Similarly, *M. birostris* abundances were not associated with temperature ($\chi^2 = 0.818$, $df = 1$, $p = 0.366$), chlorophyll-a concentration ($\chi^2 = 1.407$, $df = 1$, $p = 0.236$), or photoperiod ($\chi^2 = 1.035$, $df = 1$, $p = 0.310$) over the same period (Fig. 3b).

Discussion

This study employed aerial surveys to quantify the spatial and temporal abundance of *A. narinari* and

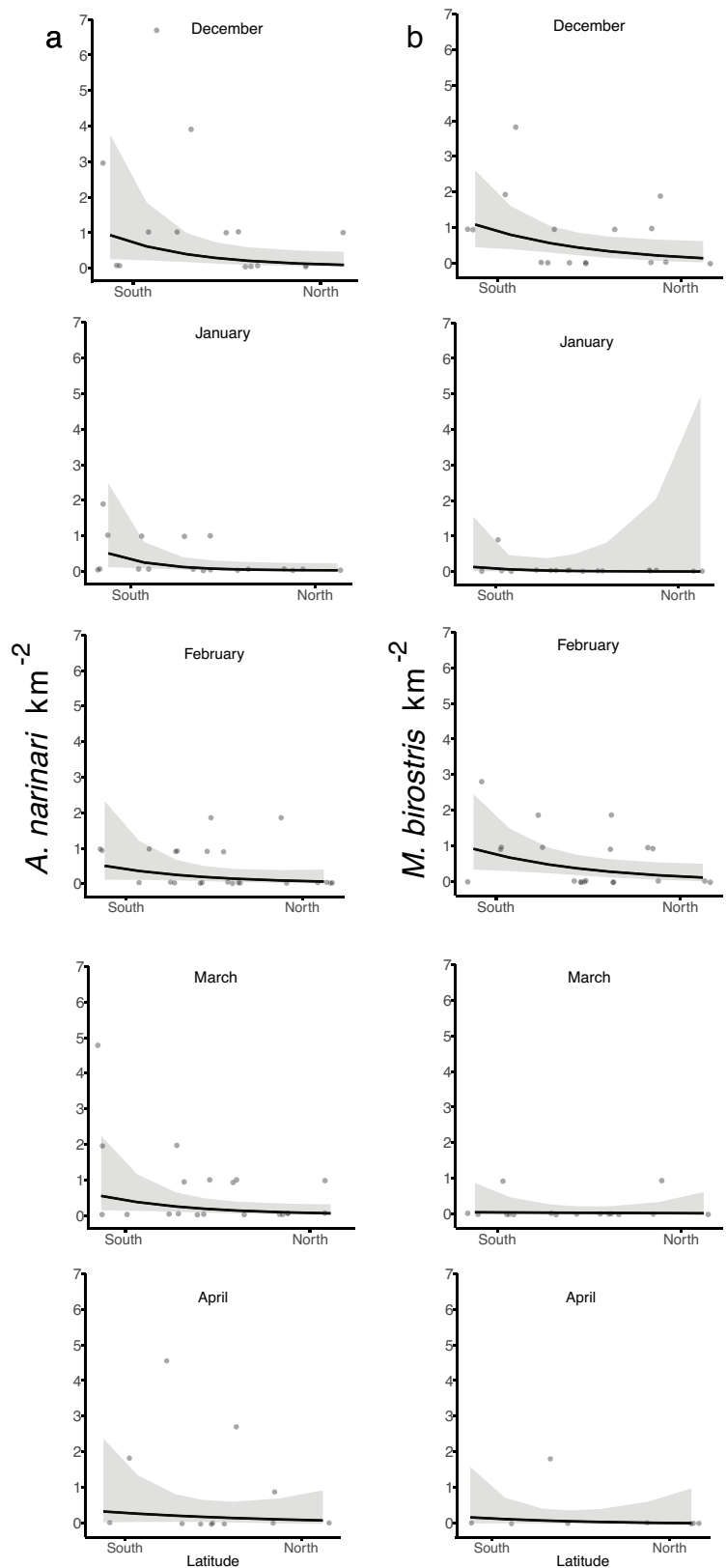
M. birostris in southeast Florida. The large body size of both species makes them suitable for aerial observation, and one or both species were seen on nearly every flight (97.5%). Aerial surveys have been used previously to successfully quantify the abundance and distribution of *M. birostris* (Girondot et al. 2015; Armstrong et al. 2020; Trujillo-Cordova et al. 2020) and *A. narinari* (Bassos-Hull et al. 2014). However, this is the first long-term (8-year) study to repeatedly sample an area where both species are seen in abundance and for which a nursery area is proposed for *M. birostris* (Pate and Marshall 2020). This allows for multi-year comparisons of the distribution of both species.

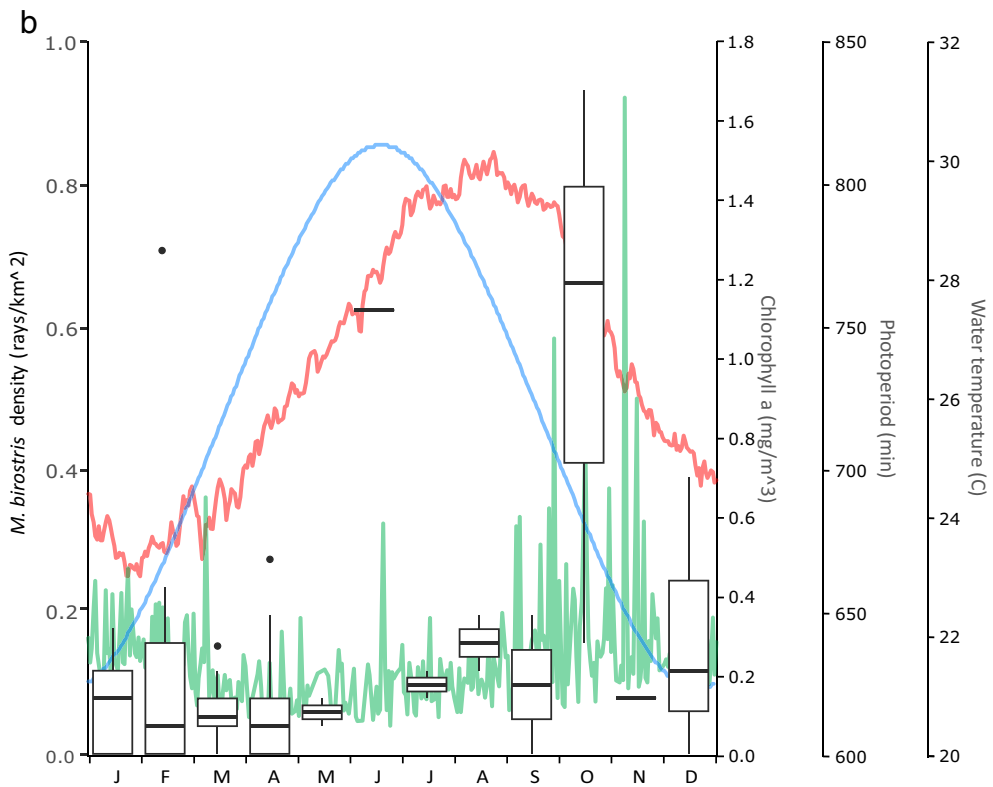
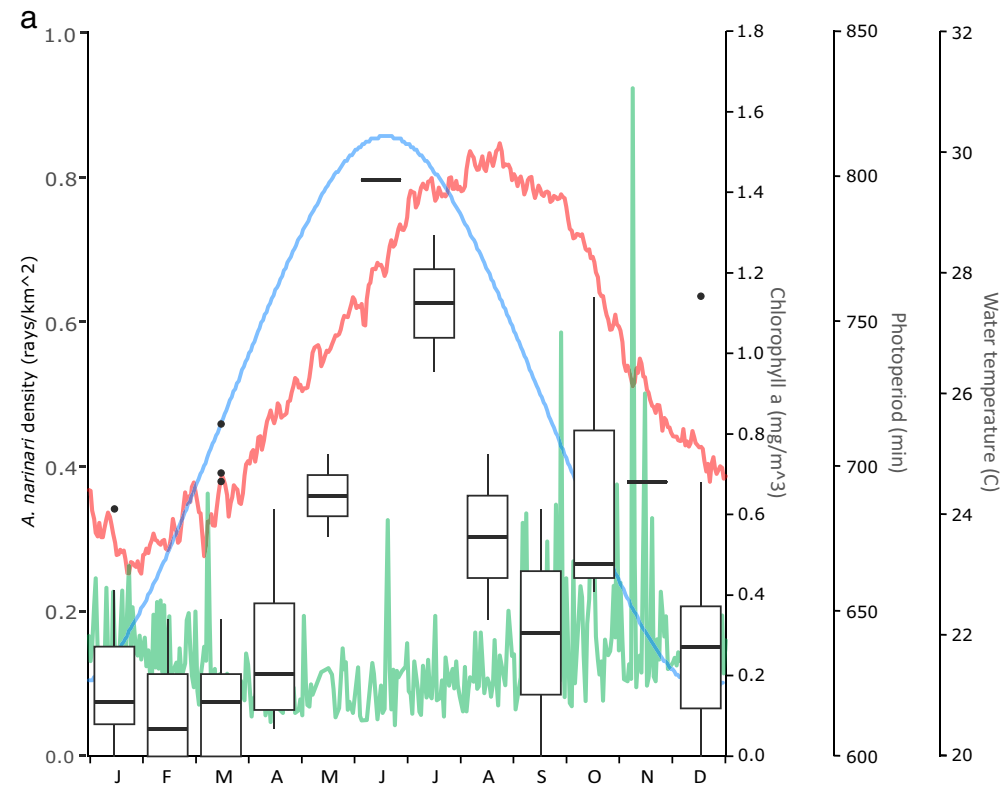
A caveat for the results reported is that the statistical analyses were conducted only for data collected from December to April each year. Since the purpose of the survey was to quantify the abundance of blacktip sharks during the overwintering period of their migration, there was minimal sampling outside of those months. Because of the limited sampling from May to November, those months were excluded from the analyses. As a result, the environmental parameters examined (water temperature, chlorophyll-a concentration, photoperiod) did not differ as widely over that limited period as they would over an entire year. Therefore, care should be taken in the interpretation of these results given the limited scope of testing.

Spatiotemporal distribution

We examined the abundance of both species across spatial (latitude) and temporal (month, year) parameters. We found that the abundance of *A. narinari* did not differ along a latitudinal gradient, but *M. birostris* was more abundant at lower latitudes (Fig. 2). Recent work on *M. birostris* in southeast Florida has been focused primarily from Boynton Beach Inlet northward (Fig. 1) (Pate and Marshall 2020; Pate et al. 2021). This area has been proposed as a nursery habitat for juvenile *M. birostris* (Pate and Marshall 2020). Given that this species is more abundant at lower latitudes, it would be worthwhile to increase sampling efforts from Ft Lauderdale to Miami. Interestingly, although the Ft Lauderdale to Miami area has a greater human population density than farther north, this does not seem to deter either species.

Fig. 2 Spatial abundance of **a** *A. narinari* and **b** *M. birostris* across latitude from Government Cut (south) to Jupiter Inlet (north). *Aetobatus narinari* showed no difference in abundance across latitudes. *Manta birostris* were more abundant at lower latitudes. Individual data points are on a gradient by year from light grey (2014) to black (2022).





◀**Fig. 3** Abundance of **a** *A. narinari* and **b** *M. birostris* with water temperature (red), photoperiod (blue), and chlorophyll-a (green) concentration. Neither species showed a significant correlation between abundance and any of the environmental variables in the months of December to April; no statistical analyses were performed for the months of May to November. For each abundance estimate, the horizontal line is the median, the box bounds the upper and lower quartiles, the whiskers are the minimum and maximum values excluding outliers, and the dots are outliers, defined as more than 1.5× the upper quartile value.

The abundance of each species was compared among months from December to April. The abundance of *A. narinari* did not differ across months for December to April (Fig. 3a), but the median number of rays appeared greater in May to November, although this was not tested statistically. When compared among months from December to April, *M. birostris* was more abundant in December and February (Fig. 3b). In addition, there appeared to be a greater abundance in October, but again, this was not tested statistically due to the small sample size. Although the data were not statistically analyzed for the period from May to November, rays were still sighted on flights during those months. The year-round presence of *M. birostris* is also indicative of a potential nursery habitat for this species in southeast Florida, as suggested by Pate and Marshall (2020). In addition, their presence close in the nearshore environment makes them susceptible to injuries caused by human interactions, including boat propeller injuries and entanglement with fishing gear (Pate and Marshall 2020; Pate et al. 2021). Despite a greater sampling effort from December to April, a greater number of animals was counted in July to October. This suggests that if the sampling effort were uniform throughout the year, the summer and autumn would likely reveal a much greater abundance of these two species. This accords with boat-based surveys of *M. birostris* in southeast Florida that found greater numbers of rays in the summer and autumn months (Pate and Marshall 2020).

The multi-year duration of this study permitted comparisons across years. Although some years had a greater number of animals observed, there was no difference in abundance across the study period for either species. This suggests that the populations of both species appear stable in southeast Florida.

Environmental correlates

Various abiotic factors, such as salinity, pH, tidal cycle, and water temperature, have been demonstrated to correlate with movements of elasmobranchs (Schlaff et al. 2014). The species will typically seek out or remain within their preferred environmental conditions. The three environmental parameters examined in this study, water temperature, chlorophyll-a concentration, and photoperiod, are all correlated and thus not independent. Longer photoperiods can lead to increased water temperatures which can contribute to greater chlorophyll-a concentrations. *Mobula birostris* are planktivores and feed at a lower trophic level than *A. narinari*. As a result, it might be expected that *M. birostris* abundance would track more closely with chlorophyll-a concentration as an indicator of primary productivity. However, no significant relationship was found between *M. birostris* abundance and chlorophyll-a concentration. Similarly, no relationship was found between *A. narinari* abundance and chlorophyll-a concentration, and none was expected. The daily chlorophyll-a concentration remained low across the tested months but appeared to peak from September to November, and that corresponded with the greater median abundance of *M. birostris* in October (Fig. 3b). However, this was not tested statistically. Other studies have reported a relationship between chlorophyll-a concentration and *M. birostris* density (Garzon et al. 2021; Farmer et al. 2022). In this study, the range of chlorophyll-a concentrations did not differ from December to April, or across years. With such a limited range of chlorophyll-a values during those months it is not surprising that no relationship was found between chlorophyll-a concentration and *M. birostris* density.

The abundance of *M. birostris* and *A. narinari* did not correlate with water temperature from December to April. The average difference in water temperature among those months was only 2.9 °C, whereas the average annual temperature range was 8.5 °C. If we had been able to test over the entire annual temperature range, differences in abundance might have been found. From the literature, *A. narinari* are found more often when water temperatures are warmer and are absent when water temperatures are cooler (Bassos-Hull et al. 2014; DeGroot et al. 2021). These results accord with the observations in this study that appeared to show generally lower abundances of *A.*

narinari during the cooler months (Dec-Apr) and increasing numbers as the water warmed (May-Jul). Interestingly, the months with some of the warmest water temperatures (Aug-Oct) did not have the greatest number of *A. narinari*. This phenomenon has also been documented for this species in southwest Florida (Bassos-Hull et al. 2014) and the Bahamas (Silliman and Gruber 1999). It has been proposed that *A. narinari* may have an upper thermal limit and when water temperatures exceed that mark the rays may shift to cooler, deeper waters (Bassos-Hull et al. 2014). Alternatively, the reduced numbers of *A. narinari* sighted during Aug-Oct might be attributable to the limited sampling during those periods.

The final environmental variable examined was photoperiod. Photoperiod has been found to correlate with movement of various elasmobranchs, typically serving as a cue to stimulate migration (Schlaff et al. 2014). For example, the cownose ray, *Rhinoptera bonasus* (Mitchill, 1815), is a member of the order Myliobatiformes, like *M. birostris* and *A. narinari*. *Rhinoptera bonasus* is more likely to be present off Chesapeake Bay during longer photoperiods and more likely to be present off Cape Canaveral during shorter photoperiods (Bangley et al. 2021). However, there was no correlation between photoperiod and abundance for either *M. birostris* or *A. narinari*. The tested period included the winter solstice and vernal equinox but did not extend to the summer solstice. Although there appears to be a greater abundance of *A. narinari* around the summer solstice (Fig. 3a), additional sampling is required to test this statistically.

Species identification

Although efforts were made to fly on days in which the waves were minimized, this was not always possible. As a result, on some days, the waves created surface distortion which made it difficult to positively identify some of the batoids to species. In some instances, we were able to determine that the specimen was either *A. narinari* or *M. birostris*, but the generally similar rhomboid body shape of these two species precluded positive identification. The maximum size of *A. narinari* (230 cm disc width; Last et al. 2016) overlaps with the minimum size of *M. birostris* in Southeast Florida (<200 cm disc width;

Pate and Marshall 2020), so size could not always be used as a distinguishing factor. As a result, other morphological features, such as the presence of cephalic lobes on *M. birostris*, were necessary to distinguish the species.

In some instances, we were able to determine that the specimen was a batoid, but were unable to identify it further. It is possible that some of the unidentified batoids were southern stingrays, *Hypanus americanus* (Hildebrand and Schroeder 1928). That species is the only other batoid in the region that occurs close to shore and grows to a sufficient size (>1 m disc width) to be spotted from an aerial survey. The light dorsal coloration of *H. americanus* allows it to blend in with the sandy seafloor, which made it difficult to see in the footage. As a result, the aerial survey no doubt underestimates their true abundance. That same light coloration, coupled with the more rounded body shape, helped to make *H. americanus* generally distinguishable from the darker colored and more rhomboid shaped *A. narinari* and *M. birostris*.

Interestingly, we did not observe any cownose rays, *R. bonasus*, on any of our survey flights. Cownose rays have been documented from various aerial surveys (Rogers et al. 1990; Blaylock 1993; Ajemian and Powers 2016) including in the Gulf of Mexico in southwest Florida where they form massive aggregations that are easily seen from the air (Clark 1963). The only other batoid that was observed was the smalltooth sawfish, *Pristis pectinata* Latham, 1794. Individuals of this species were spotted on only two survey flights. Their elongated rostrum made them instantly recognizable, but their light coloration allowed them to blend in with the seafloor. Like *H. americanus*, it is possible that we underestimated their actual abundance.

The number of animals counted represents only those that were within about 200 m of the shoreline, which is characterized by water less than 4 m deep within the study area. In some instances, the animals were very close to the beach with *M. birostris* being seen within 1–2 disc widths from the shore. Their dorso-ventrally compressed body may enable even large batoids to enter such shallow water. Shallow water refugia has been documented in blacktip sharks that escape to the surf zone when pursued by large great hammerhead sharks (Doan and Kajiura 2020). Even large *M. birostris* are preyed upon by large sharks that can inflict significant bite wounds

(Marshall and Bennett 2010). It is possible that *M. birostris* may seek refuge from large predatory sharks that might not be able to swim and maneuver in the shallow water adjacent to the beach.

Conservation implications

Populations of chondrichthyan fishes are declining worldwide, in some cases dramatically (Dulvy et al. 2014). Among those in greatest peril are the largest species, especially those found in shallow water accessible to fishermen (Dulvy et al. 2014). This includes both of the batoid species in this study. *Aetobatus narinari* is suspected of having declined by 50–79% throughout its range in the past 30 years, which has resulted in it being classified as Endangered by the IUCN (Dulvy et al. 2021). However, in US waters and the Caribbean islands, where there is no fishery for this species, it is of Least Concern (Dulvy et al. 2021). The same applies to *M. birostris* which has experienced population declines of 50–79% globally, but sighting trends remain stable in areas where they are protected, including the USA (Marshall et al. 2022).

In 2018, *M. birostris* was listed as Threatened under the Endangered Species Act and the National Marine Fisheries Service was tasked with developing a recovery plan (NOAA 2018; NOAA 2019). Until that time, general recovery guidelines have been incorporated into a domestic action plan. Some of these items include improved understanding of the population distribution and abundance, identifying and protecting key habitat areas, and understanding movement and seasonal distributions (NOAA 2020). The seasonal abundance and distribution data presented in this study may contribute valuable information that can be used in the effective management of both of these charismatic species.

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Author contribution Conceived and designed the experiments: SMK. Performed the experiments: SMK, JMW. Analyzed the data: SMK, JMW, MLM. Wrote the manuscript: SMK, MLM.

Data availability Data will be made available upon reasonable request.

Declarations

Ethical approval This study was observational and did not involve any contact or interaction with animals, so an IACUC protocol was not required.

Conflict of interest The authors declare no competing interests.

References

- [NOAA] (2018) National Oceanographic and Atmospheric Administration Fisheries Service. Final rule to list the giant manta ray as threatened under the endangered species act. Federal Register 83:2916–2931.
- [NOAA] (2019) National Oceanographic and Atmospheric Administration Fisheries Service. Determination on the designation of critical habitat for giant manta ray. Federal Register 84:66652–66664.
- [NOAA] (2020) National Oceanographic and Atmospheric Administration Fisheries Service. Giant manta ray recovery outline. Office of Protected Resources. <https://www.fisheries.noaa.gov/resource/document/giant-manta-ray-recovery-outline> Accessed 07 February 2023
- Ajemian MJ, Powers SP (2016) Seasonality and ontogenetic habitat partitioning of cownose rays in the northern Gulf of Mexico. *Estuar Coast* 39(4):1234–1248. <https://doi.org/10.1007/s12237-015-0052-2>
- Armstrong AJ, Armstrong AO, Bennett MB, McGregor F, Abrantes KG, Barnett A, Richardson AJ, Townsend KA, Dudgeon CL (2020) The geographic distribution of reef and oceanic manta rays (*Mobula alfredi* and *Mobula birostris*) in Australian coastal waters. *J Fish Biol* 96(3):835–840. <https://doi.org/10.1111/jfb.14256>
- Bangley CW, Edwards ML, Mueller C, Fisher RA, Aguilar R, Heggie K, Richie K, Ahr BJ, Ogburn MB (2021) Environmental associations of cownose ray (*Rhinoptera bonasus*) seasonal presence along the U.S. Atlantic Coast. *Ecosphere* 12(9):e03743. <https://doi.org/10.1002/ecs2.3743>
- Bassos-Hull K, Wilkinson KA, Hull PT et al (2014) Life history and seasonal occurrence of the spotted eagle ray, *Aetobatus narinari*, in the eastern Gulf of Mexico. *Environ Biol Fish* 97:1039–1056. <https://doi.org/10.1007/s10641-014-0294-z>
- Bauer RK, Bonhommeau S, Brisset B, Fromentin JM (2015) Aerial surveys to monitor bluefin tuna abundance and track efficiency of management measures. *Mar Ecol Prog Ser* 534:221–234. <https://doi.org/10.3354/meps11392>
- Blaylock RA (1993) Distribution and abundance of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries* 16(2):255–263. <https://doi.org/10.2307/1352498>
- Brewster LR, Cahill BV, Burton MN et al (2021) First insights into the vertical habitat use of the whitespotted eagle ray *Aetobatus narinari* revealed by pop-up satellite archival tags. *J Fish Biol* 98:89–101. <https://doi.org/10.1111/jfb.14560>

- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9(2):378–400. <https://doi.org/10.32614/RJ-2017-066>
- Certain G, Bretagnolle V (2008) Monitoring seabirds population in marine ecosystem: the use of strip-transect aerial surveys. *Remote Sens Environ* 112(8):3314–3322. <https://doi.org/10.1016/j.rse.2008.01.019>
- Chung Y, Rabe-Hesketh S, Dorie V, Gelman A, Liu J (2013) A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika* 78(4):685–709. <https://doi.org/10.1007/s11336-013-9328-2>
- Churnside JH, Sharov AF, Richter RA (2011) Aerial surveys of fish in estuaries: a case study in Chesapeake Bay. *ICES J Mar Sci* 68:239–244. <https://doi.org/10.1093/icesjms/fsq138>
- Clark E (1963) Massive aggregations of large rays and sharks in and near Sarasota, Florida. *Zoologica* 48(2):61–64. <https://doi.org/10.5962/p.203310>
- DeGroot BC, Bassos-Hull K, Wilkinson KA et al (2021) Variable migration patterns of whitespotted eagle rays *Aetobatus narinari* along Florida's coastlines. *Mar Biol* 168(2):18. <https://doi.org/10.1007/s00227-021-03821-2>
- DeGroot BC, Roskar G, Brewster L, Ajemian MJ (2020) Fine-scale movement and habitat use of whitespotted eagle rays *Aetobatus narinari* in the Indian River Lagoon, Florida, USA. *Endang Species Res* 42:109–124. <https://doi.org/10.3354/esr01047>
- Doan MD, Kajiura SM (2020) Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*). *J Fish Biol* 96:1530–1533. <https://doi.org/10.1111/jfb.14342>
- Dulvy NK, Carlson J, Charvet P, Ajemian MJ, Bassos-Hull K, Blanco-Parra MP, Chartrain E, Derrick D, Dia M, Diop M, Doherty P, Dossa J, De Bruyne G, Herman K, Leurs GHL, Mejía-Falla PA, Navia AF, Pacoureau N, Pérez Jiménez JC, Pires JD, Seidu I, Soares AL, Tamo A, VanderWright WJ, Williams AB (2021) *Aetobatus narinari* (amended version of 2021 assessment). The IUCN Red List of Threatened Species 2021: e.T42564343A201613657. <https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T42564343A201613657.en> Accessed 07 February 2023
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP, Pollock CM, Simpfendorfer CA, Burgess GH, Carpenter KE, Compagno LJ, Ebert DA, Gibson C, Heupel MR, Livingstone SR et al (2014) Extinction risk and conservation of the world's sharks and rays. *Elife* 3:e00590. <https://doi.org/10.7554/eLife.00590>
- Edwards HH, Pollock KH, Ackerman BB, Reynolds JE, Powell JA (2007) Estimation of detection probability in manatee aerial surveys at a winter aggregation site. *J Wildl Manage* 71(6):2052–2060. <https://doi.org/10.2193/2005-645>
- Elston DA, Moss R, Bouliner T, Arrowsmith C, Lambin X (2001) Analysis of aggregation, a worked example: number of ticks on red grouse. *Parasitology* 122:563–569. <https://doi.org/10.1017/S0031182001007740>
- Farmer NA, Garrison LP, Horn C et al (2022) The distribution of manta rays in the western North Atlantic Ocean off the eastern United States. *Sci Rep* 12:6544. <https://doi.org/10.1038/s41598-022-10482-8>
- Fox J, Weisberg S (2019) An {R} companion to applied regression, Third Edition. Sage, Thousand Oaks CA
- Garzon F, Graham RT, Witt MJ, Hawkes LA (2021) Ecological niche modeling reveals manta ray distribution and conservation priority areas in the Western Central Atlantic. *Anim Conserv* 24(3):322–334. <https://doi.org/10.1111/acv.12663>
- Gilmore RG (1977) Fishes of the Indian River Lagoon and adjacent waters, Florida. *Bull Fla State Mus Biol Sci* 22:101–148
- Girondot M, Bédél S, Delmoitiez L, Russo M, Chevalier J, Guéry L, Hassine SB, Féon H, Jribi I (2015) Spatio-temporal distribution of *Manta birostris* in French Guiana waters. *J Mar Biol Assoc UK* 95(1):153–160. <https://doi.org/10.1017/S0025315414001398>
- Hartig F (2022) DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMA>.
- Kajiura SM, Tellman SL (2016) Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in southeast Florida. *PLoS One* 11(3):e0150911. <https://doi.org/10.1371/journal.pone.0150911>
- Kiszka JJ, Heithaus MR (2019) Using aerial surveys to investigate the distribution, abundance, and behavior of sharks and rays. In: Carrier JC, Heithaus MR, Simpfendorfer CA (eds) *Shark research: emerging technologies and applications for the field and laboratory*. CRC Press, Boca Raton, FL, pp 71–82. <https://doi.org/10.1201/b21842>
- Last PR, White WT, deCarvalho MR, Seret B, Stehmann MFW, Naylor GJP (2016) Rays of the world. CSIRO Publishing. <https://doi.org/10.1071/9780643109148>
- Lauriano G, Panigada S, Casale P, Pierantonio N, Donovan G (2011) Aerial survey abundance estimates of the loggerhead sea turtle *Caretta caretta* in the Pelagos Sanctuary, northwestern Mediterranean Sea. *Mar Ecol Prog Ser* 437:291–302. <https://doi.org/10.3354/meps09261>
- Lüdecke D (2018) ggeffects: Tidy data frames of marginal effects from regression models. *JOSS* 3(26):772. <https://doi.org/10.21105/joss.00772>
- Lutcavage M, Kraus S, Hoggard W (1997) Aerial survey of giant bluefin tuna, *Thunnus thynnus*, in the Great Bahama Bank, Straits of Florida, 1995. *Fish Bull* 95:300–310
- Lynn K, Porzio D, Kesaris A (2014) Aerial sardine surveys in the Southern California Bight. *CFWJ* 100(2):260–275
- Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Derrick D, Herman K, Jabado RW, Liu KM, Rigby CL, Romanov E (2022) *Mobula birostris* (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2022: e.T198921A214397182. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T198921A214397182.en> Accessed 07 February 2023
- Marshall AD, Bennett MB (2010) The frequency and effect of shark-inflicted bite injuries to the reef manta ray *Manta alfredi*. *African J Mar Sci* 32(3):573–580. <https://doi.org/10.2989/1814232X.2010.538152>

- Pate JH, Macdonald C, Wester J (2021) Surveys of recreational anglers reveal knowledge gaps and positive attitudes towards manta ray conservation in Florida. *Aquat Conserv Mar Freshw Ecosyst* 31(6):1410–1419. <https://doi.org/10.1002/aqc.3508>
- Pate JH, Marshall AD (2020) Urban manta rays: potential manta ray nursery habitat along a highly developed Florida coastline. *Endang Species Res* 43:51–64. <https://doi.org/10.3354/esr01054>
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>
- Robbins WD, Peddemors VM, Kennelly SJ, Ives MC (2014) Experimental evaluation of shark detection rates by aerial observers. *PLoS One* 9(2):e83456. <https://doi.org/10.1371/journal.pone.0083456>
- Rogers C, Roden C, Lohoefer R, Mullin K, Hoggard W (1990) Behavior, distribution, and relative abundance of cownose ray schools *Rhinoptera bonasus* in the northern Gulf of Mexico. *Northeast Gulf Sci* 11:69–76
- Sales JBL, de Oliveira CN, dos Santos WCR et al (2019) Phylogeography of eagle rays of the genus *Aetobatus*: *Aetobatus narinari* is restricted to the continental western Atlantic Ocean. *Hydrobiologia* 836:169–183. <https://doi.org/10.1007/s10750-019-3949-0>
- Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. *Rev Fish Biol Fish* 24:1089–1103. <https://doi.org/10.1007/s11160-014-9364-8>
- Silliman WR, Gruber SH (1999) Behavioral ecology of the spotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790), in Bimini, Bahamas: an interim report. *Bahamas J Sci B* 7(1):13–20
- Smultea M, Smultea J, Thomas A (2014) Changes in relative occurrence of cetaceans in the Southern California Bight: a comparison of recent aerial survey results with historical data sources. *Aquat Mamm* 40(1):32–43. <https://doi.org/10.1578/AM.40.1.2014.32>
- Snelson FF, Williams SE (1981) Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River Lagoon System, Florida. *Estuaries* 4:110–120
- Trujillo-Cordova JA, Mimila-Herrera E, Cardenas-Paloma N, Herrera-Silveira JA (2020) 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. *Fish Bull* 118:240–249. <https://doi.org/10.7755/FB.118.3.3>
- Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer, New York
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*, vol 574. Springer, New York

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