

Observations of spotted eagle rays (*Aetobatus narinari*) in the Mexican Caribbean using photo-ID

F. Cerutti-Pereyra · K. Bassos-Hull ·
X. Arvizu-Torres · K. A. Wilkinson ·
I. García-Carrillo · J. C. Perez-Jimenez · R. E. Hueter

Received: 25 March 2017 / Accepted: 30 October 2017
© Springer Science+Business Media B.V., part of Springer Nature 2017

Abstract The spotted eagle ray is an iconic species for the recreational diving and snorkeling industry in the Mexican Caribbean although it is heavily fished in nearby waters of the southern Gulf of Mexico and in Cuba. This species is listed on the IUCN Red List of Threatened Species as ‘Near Threatened’ with a decreasing population trend. Few studies have reported on the populations and migrations of spotted eagle rays in the Atlantic Ocean, Gulf of Mexico and Caribbean Sea, and no regulations currently exist for the fishery or tourism industries in Mexico. Photographic identification techniques were used to produce the first photo-ID

catalog of spotted eagle rays in the Mexican Caribbean using 1096 photographs submitted by researchers and divers between 2003 and 2016. In total, 282 individual spotted eagle rays were identified through photographs at nine sites across the Mexican Caribbean. Of these individuals, 14.9% were resighted at least once at the same site. The longest period between re-sighting events was 342 days. This is the first study evaluating free-swimming spotted eagle rays in the Mexican Caribbean and highlights the value of using photo-ID for monitoring populations of this ray. Because a targeted subsistence fishery for spotted eagle rays exists in nearby waters, management efforts to monitor and prevent overexploitation at key diving locations should be a priority for local government agencies.

F. Cerutti-Pereyra (✉) · X. Arvizu-Torres ·
I. García-Carrillo
Blue Core A.C, Calle 25 entre 26/28, Miguel Alemán,
97148 Mérida, Yucatán, Mexico
e-mail: florenciacp@gmail.com

K. Bassos-Hull · R. E. Hueter
Center for Shark Research, Mote Marine Laboratory, Sarasota, FL
34236, USA

K. A. Wilkinson
Sarasota Dolphin Research Program, Chicago Zoological Society
c/o Mote Marine Laboratory, 1600 Ken Thompson Parkway,
Sarasota, FL 34236, USA

K. A. Wilkinson
School of Natural Resources and Environment, University of
Florida, 103 Black Hall, PO Box 116455, Gainesville, FL 32611,
USA

J. C. Perez-Jimenez
El Colegio de la Frontera Sur (ECOSUR), Av. Rancho Polígono
2-A, Ciudad Industrial, CP. 24500 Lerma, Campeche, Mexico

Keywords *Aetobatus narinari* · Spotted eagle ray ·
Caribbean · Mexico · Photo-ID · Site fidelity ·
Aggregation · Batoid

Introduction

The spotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790), is a highly mobile ray found in coastal tropical waters, often in coral reef and estuarine bay habitats. This ray is relatively long-lived with low fecundity (1–4 pups) and late sexual maturity at 4–6 yrs. (Last and Stevens 2009; Bassos-Hull et al. 2014). This species of ray feeds primarily on bivalves and gastropod mollusks (Ajemian et al. 2012). Iversen et al. (1986) and Randall (1964) found the queen conch, *Strombus gigas*

(Linnaeus, 1758), may be dominant in their diet in the Caribbean and Bahamas.

Recent molecular analysis indicate there are more than one species of spotted eagle ray and possibly up to seven different species (Naylor et al. 2005; Richards et al. 2009; Schluessel et al. 2010b; White et al. 2010). Spotted eagle rays in the western and central Pacific were recently reclassified as *Aetobatus ocellatus* (Richards et al. 2009; White et al. 2010). Caribbean and Gulf of Mexico spotted eagle rays are currently considered to be the same species, *A. narinari*. With recent taxonomic changes within the species complex, the conservation status needs to be reviewed and updated on local and regional scales.

Spotted eagle rays face a variety of challenges to the sustainability of their populations. This species is targeted in fisheries throughout their range for human consumption (Dubick 2000; Schluessel et al. 2010a; Tagliafico et al. 2012), including a targeted fishery in the southern Gulf of Mexico (Cuevas-Zimbrón et al. 2011). Spotted eagle rays are listed as ‘Near Threatened’ by the IUCN Red List, with a decreasing population trend in most of its range and ‘Vulnerable’ in Southeast Asia, primarily due to local fisheries impacts (Kyne et al. 2006). Additionally, their prey items are often associated with reef and coastal environments, both habitats under threat from pollution and urbanization (Burke et al. 2011).

Successful management and conservation of wildlife requires a good understanding of how species use the habitat, how geographically separated populations may be connected, and how or if species are resident to certain locations (Klimley and Butler 1988; Andrews et al. 2007; Jorgensen et al. 2009). Photo-identification (photo-ID) using distinctive markings to identify individuals has become popular among researchers for certain species since it is a reliable, non-invasive and less expensive technique compared to other tools like tagging. For these reasons, photo-ID has become a useful tool for studying various species of sharks (Bonfil et al. 2005; Van Tienhoven et al. 2007; Davies et al. 2012) and rays (Corcoran and Gruber 1999; Couturier et al. 2011; Marshall et al. 2011; Bassos-Hull et al. 2014; González-Ramos et al. 2016). Species that are good candidates for photo-ID show a distinctive and persistent pattern of markings and are predictably found in certain localities (Marshall et al. 2011). Spotted eagle rays have natural and persistent markings on their dorsal surface that allow visual identification of individuals (Corcoran and Gruber 1999; Bassos-Hull et al. 2014; González-Ramos et al. 2016).

The Mexican Caribbean is one of Latin America’s most important tourism destinations where the main attraction is the enjoyment of the beach and coastal waters, and where recreational diving is a popular activity (Córdoba-Ordoñez and García 2003; CONCANACO and SERVITUR 2016). During the winter season (December – March), spotted eagle rays gather in groups in popular dive sites and are a charismatic species for recreational divers and snorkelers (Cerutti-Pereyra, Arvizu-Torres, and García-Carrillo, pers. obs.). Other species of rays, such as mantas (*Mobula alfredi*) show site fidelity in which the same individual visits to the same site multiple times across years (Marshall 2008; Couturier et al. 2011; Flowers et al. 2016) and spotted eagle rays are thought to show this behavior in other areas of the Atlantic Ocean (Ajemian and Powers 2014; Bassos-Hull et al. 2014). However, it is unknown if these rays are visiting the same areas of the Mexican Caribbean where they are an important attraction for tourism.

Populations of spotted eagle rays have shown signs of declines in the western Atlantic for more than a decade (Correa and Manjarrés 2004; Tagliafico et al. 2012), including in the neighboring waters of the Gulf of Mexico (Shepherd and Myers 2005; Cuevas-Zimbrón et al. 2011). Fishery regulations in Mexico only control the fishing gear that is permitted via fishing licenses (polyamide multifilament gill-nets with 30–40 cm mesh size) (DOF 2012). The biological traits of spotted eagle rays, the intensive fishery they support, and the impacts on their habitat make them extremely vulnerable to over-exploitation. Despite this, little is known about their populations, movements, site fidelity, or habitat use in the Mexican Caribbean. Baseline information on this species is critical to understand the impacts of fisheries and tourism on this ray and to assess the need for fishery and tourism regulations in the area. Therefore, this study aims to describe the aggregations and movements of spotted eagle rays using photo-ID in key sites for tourism and recreation in the Mexican Caribbean.

Methods

Study sites

The Mexican Caribbean refers to the marine waters on the east coast of tropical Mexico, in the state of Quintana Roo (QR) (Fig. 1). In the Mexican Caribbean, spotted

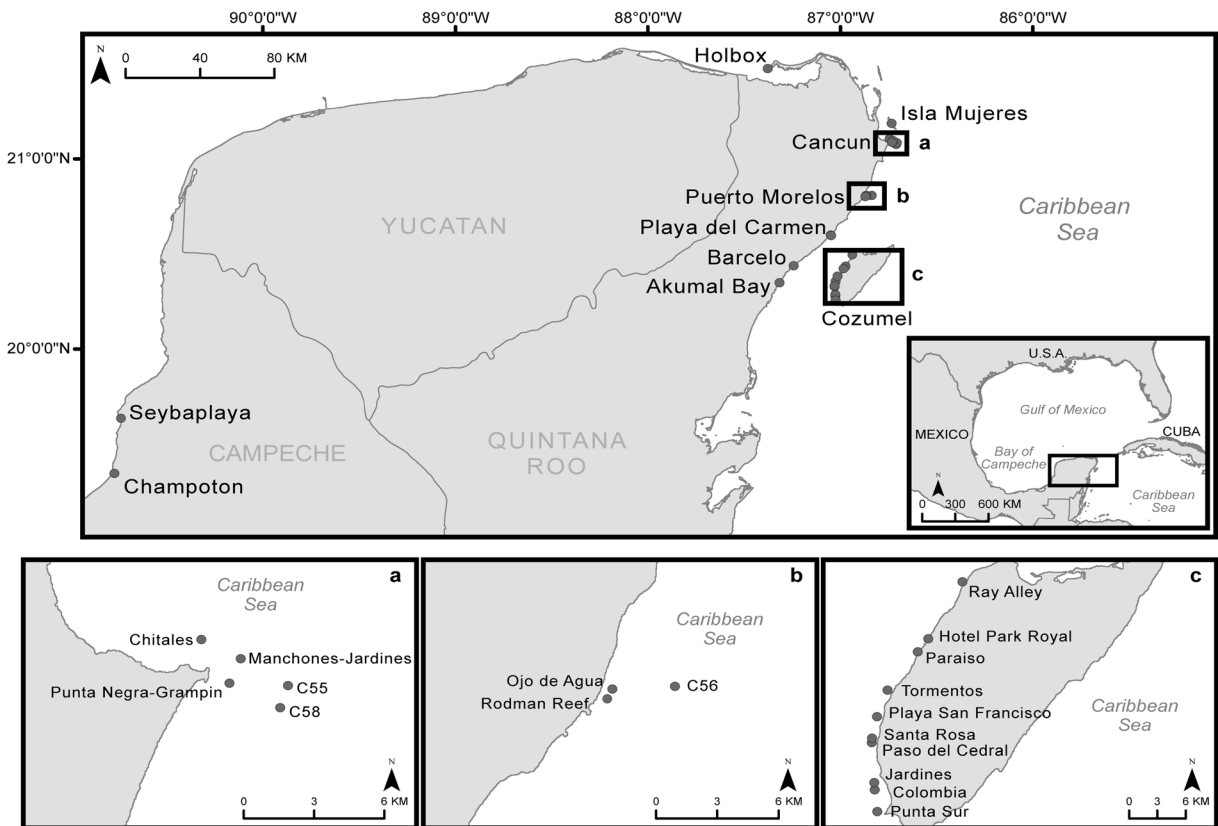


Fig. 1 Map of the Mexican Caribbean and neighboring state of Campeche indicating locations of monitored sites

eagle rays have been observed in large groups (25–30 individuals) at popular tourist sites with depths of 18–30 m and single individuals along the coast at depths of 1–10 m (Cerutti-Pereyra, Arvizu-Torres, and García-Carrillo, pers. obs.). The shipwrecks C-58 at 30 m max depth and the C-55 at 30 m max depth are scuba diving sites used year-round, with strong currents during the winter, good visibility, and diverse marine life (Fig. 1a). Those were the principal study sites for data collection as they are popular amongst divers due the spotted eagle ray aggregations and are readily accessible by boat with commercial tour operations.

Data collection

A Citizen Science and Outreach Program (CSOP) was launched in Mexico prior to the winter 2015 season by Blue Core A.C., a non-governmental conservation organization. This program aimed to collect historical photographs of spotted eagle rays from the community of dive instructors, underwater photographers, recreational divers and snorkelers. Photographs of spotted eagle rays were

obtained from various locations throughout QR through this program, as well as by Blue Core A.C. during winter season from December 2015 to March 2016. Photographs of spotted eagle rays caught in targeted fisheries were collected from two sites (Isla Mujeres and Holbox, Fig. 1) within QR. Additionally, colleagues from El Colegio de la Frontera Sur (ECOSUR) provided photographs from two fishery camps in the neighboring state of Campeche (southern Gulf of Mexico).

Sampling effort was opportunistic, as much of the data were obtained by a network of citizen scientists in popular scuba diving/snorkeling sites visited often by recreational divers. These popular dive sites included: Akumal (Fig. 1), Cancun C-58 & C-55 (Fig. 1a); Puerto Morelos C56 and Ojo de Agua (Fig. 1b); and Cozumel (Fig. 1c). Additional sites around QR had spotted eagle ray sightings which were recorded by recreational divers, but sightings were less frequent.

Underwater digital still and video cameras were used while scuba diving and snorkeling. A quality check of each photograph and video received was done prior to processing it. A photo was considered good quality if

the spots on the ray could clearly be identified when zoomed-in and if the angle was such that the spot pattern was not distorted. Photographs were not incorporated into the database if they had poor quality or angle. Each photograph that was added to the database included date, photographer, and location.

The pelvic fins and surrounding area have been suggested by other studies (Lupton 2009; González-Ramos et al. 2016) as a suitable area of the ray's body to identify and differentiate individuals (Fig. 2a). Although most spotted eagle rays were identified using several photographs from the same sighting event, a single good-quality photograph of an individual was considered sufficient for positive identification. The sex of individuals was determined when claspers were confirmed to be present (male) or absent (female) alongside pelvic fins (Fig. 2b). However, analysis related to sex-biased behaviors were not possible in this study due to the difficulty of differentiating juvenile males from females using photographs of the rays' dorsal surface. While an adult male could clearly be identified from photographs taken from the dorsal side of a spotted eagle ray, as the claspers extend beyond the length of the pelvic fins in mature males, the smaller claspers of a juvenile male were covered by the base of the tail and could not reliably be observed. Individuals were only considered female if a photograph or video clearly verifying the lack of claspers was available. If an individual could not be determined to be male or female, the sex was classified as unknown.

Photographs of pelvic fins were organized by site and date into a digital library after a quality check. Interactive Individual Identification System spot-recognition software (I3S, Spot version 4.02) (den Hartog and Reijns 2007) was used to identify individuals rays by

the shape and location of spots and compare photographs of pelvic fins within the library. This software uses a two-dimensional linear algorithm to compare number of spots, shape, position and size within a delimited area of the ray's body and has been successfully used for identification of spotted eagle rays in several studies (Lupton 2009; González-Ramos et al. 2016). It calculates the distance between spots and gives a rank for each image. A better match between compared points is shown by a lower rank when photographs are compared. A re-sighting event is defined as the identification of a known individual more than 24 h after it was last seen (Marshall 2008).

Results

In total, 1096 photographs from 120 different days between 2003 and 2016 were collected by Blue Core A.C. and a network of citizen scientists across 20 sites in QR, two fishery camps in QR, and two fishery camps in Campeche (Fig. 1 and Table 1). A total of 438 (40%) were obtained by Blue Core A.C., with the rest obtained through the CSOP. A subset of these photographs (534) was of sufficient quality and used for photo-ID. A total of 282 individuals were identified across all sites, but most were identified from Cancun and Puerto Morelos (Fig. 3). Of the 282 spotted eagle rays identified, 12.1% ($n = 34$) individuals were classified as female, 17.8% ($n = 50$) individuals were classified as male, and 70.2% ($n = 198$) were labeled as unknown.

New identifications were plotted at each locality over time in a discovery curve, based on photographs collected from all sources (Fig. 4). The discovery curve shows an increase of new individuals since 2003 with a

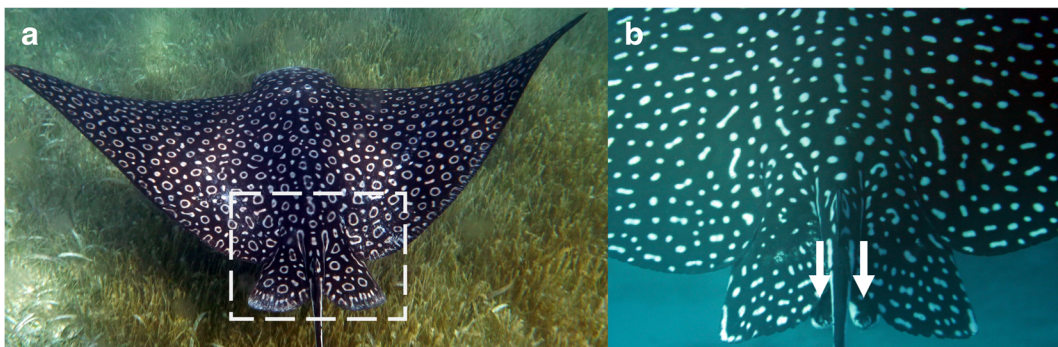


Fig. 2 Main region on spotted eagle ray's dorsal-caudal region used for photo-identification indicated by dashed line (a); sex determined by presence or absence of male claspers (b)

Table 1 Total of photographs collected across sites

Area	Site	Total number of photographs
Akumal	–	62
Barceló	–	6
Campeche	Champotón	11
Campeche	Seybaplaya	38
Cancún	C55	84
Cancún	C58	517
Cancún	Chitales Reef	2
Cancún	Manchones, Jardines	2
Cancún	Punta Negra Grampin	22
Cozumel	Colombia	16
Cozumel	Jardines	16
Cozumel	Paradise Reef	6
Cozumel	Paso del Cedral	1
Cozumel	Punta Sur	1
Cozumel	Ray Alley	4
Cozumel	San Francisco	4
Cozumel	Santa Rosa	6
Cozumel	Santa rosa bajo	5
Cozumel	Tormentos Reef	2
Cozumel	Unknown	46
Holbox	–	5
Isla Mujeres	–	4
Playa del Carmen	Moc-che Bajo	5
Playa del Carmen	Unknown	3
Puerto Morelos	C56	28
Puerto Morelos	La Pared	4
Puerto Morelos	Ojo de Agua	74
Puerto Morelos	Rodman’s Reef	13
Puerto Morelos	Unknown	105

peak in 2015. This indicates that the entire population of spotted eagle ray has not been sampled as the curve did not reach an asymptote. A large spike of identified individuals occurred in 2015 when the CSOP began and more active effort was devoted to collecting photographs taken by the community.

The longest period between multiple sighting events of a single individual was 342 days. From 282 individuals identified, 14.9% ($n = 42$) were sighted twice and several individuals were sighted three to eight times during the same season (Table 2). Two individuals (0.7%) were sighted across two consecutive winters (winters of 2015 and 2016); AN130 was first sighted

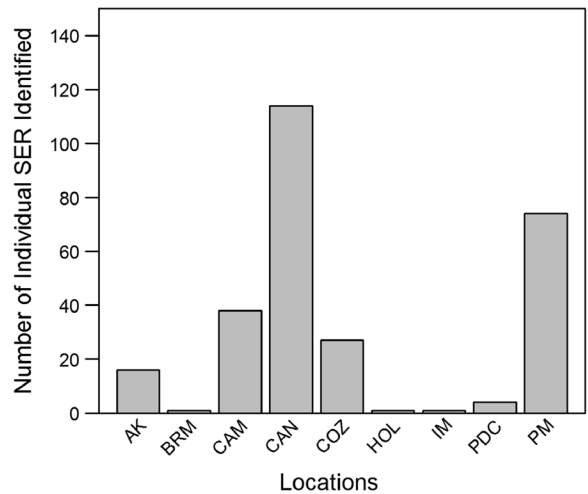


Fig. 3 Number of individual spotted eagle rays identified per site. AK = Akumal Bay, BRM = Barceló, CAM = Campeche, CAN = Cancún, COZ = Cozumel, HOL = Holbox, PDC = Playa del Carmen, PM = Puerto Morelos

during the 2015 season and then three times during the 2016 season; AN150 was first sighted in the 2015 season and then seven times during the 2016 season. All sightings of AN130 and AN150 occurred at site C58. Other individuals identified >2 times were sighted within the same season. Nine individuals (3.2%) were resighted across two near-by sites, shipwrecks C-58 and

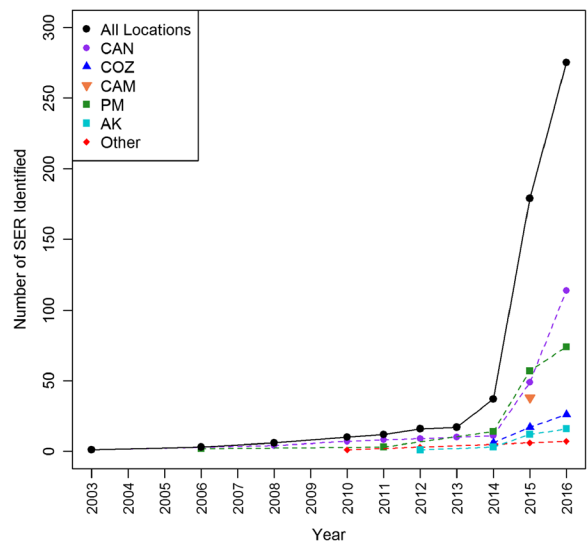


Fig. 4 Discovery curves of individual spotted eagle rays identified at all sites along the Mexican Caribbean between 2003 to 2016 (black line), and the main sites monitored during the winter season: CAN = Cancun, COZ = Cozumel, CAM = Campeche, PM = Puerto Morelos; AK = Akumal Bay, Other = shows the rest of the sites (Barceló, Playa del Carmen, and Holbox) pooled together

Table 2 Number of times individuals were sighted

Times sighted	N	%
1	282	100
2	42	14.9
3	12	4.3
4	4	1.4
5	3	1.1
6	3	1.1
7	2	0.7
8	1	0.4

C-55 in Cancun. No additional resightings across sites were reported. No animals caught in the fishing camps were identified in the photo-ID library.

Discussion

This is the first study of spotted eagle rays using photo-identification in the Mexican Caribbean. The study involved a combination of field work by trained biologists at Blue Core A.C. and voluntary collection of information through a citizen science program. While photo-ID has some limitations, such as limited temporal and spatial coverage, photo-ID can be used as an efficient tool to monitor long-term patterns when researchers involve the diving and snorkeling community through citizen science programs (Marshall and Bennett 2010; Couturier et al. 2011; Davies et al. 2012). The capacity of this research was significantly increased by the citizen science program as approximately 60% of the total photographs were provided through the CSOP.

Spotted eagle rays in this study displayed site fidelity to the shipwreck C-58 throughout a season and across years. It is important to understand when and where aggregations occur to be able to better manage key habitats used by this migratory species during their life cycle. Site fidelity or philopatry has been reported for spotted eagle rays in other localities of the western Atlantic (Silliman and Gruber 1999; Ajemian et al. 2012; Ajemian and Powers 2014; Bassos-Hull et al. 2014; Flowers et al. 2016) as well as in other ray species such as the reef manta (Dewar et al. 2008; Marshall 2008; Couturier et al. 2011), the round stingray (*Urobatis halleri*) (Vaudo and Lowe 2006), shark-like-bodied ray families Rhynchobatidae and Rhinobatidae (White et al. 2014), and various species of skates (*Raja spp*) (Ellis et al. 2011).

The popular shipwreck diving sites where spotted eagle rays are commonly seen during winter by recreational divers in the Mexican Caribbean are continuously visited throughout the year by tourists as the artificial reefs formed by shipwrecks are commonly sought after by the diving community (Edney 2006). The end of the boreal winter (March) is considered the end of the spotted eagle ray season because there is a sharp decline of spotted eagle ray sightings in dive sites despite divers visiting these sites year-round (Cerutti-Pereyra, Arvizu-Torres, and García-Carrillo, pers. obs.). A higher presence of spotted eagle rays has also been reported in the southern Gulf of Mexico and Caribbean during winter seasons (Cuevas-Zimbrón et al. 2011; Tagliafico et al. 2012). In contrast, Bassos-Hull et al. (2014) found that this species occurred more often during spring, summer and autumn in southwest Florida. Moreover, Sellas et al. (2015) found evidence of gene flow in populations of spotted eagle rays between Mexico and Cuba, and between Florida and Cuba suggesting these rays may be capable of long-term and large-scale migrations. This species likely prefers cooler water temperatures in the Gulf of Mexico during summer and moves south to warmer waters of the northwestern Caribbean Sea region as temperatures in the Gulf drop in winter. Other species of large coastal rays such as *A. flagellum* have shown seasonal variations in abundance likely related to temperature (Yamaguchi et al. 2005) and reef mantas have shown long-term migrations (Kitchen-Wheeler 2010; Couturier et al. 2012). A comparison of photo-ID libraries from Florida and Mexico and other regions of the Gulf of Mexico and Caribbean Sea is needed to confirm the hypothesis of migrations between the areas. Given the vulnerability of this species due to its life-history traits and the presence of intensive fisheries nearby, more information about the population structure and movement across sites and international boundaries is critical to understand how spotted eagle rays use the habitats within the Mexican Caribbean. Such information is crucial if regulations for fisheries and tourism are to be created and enforced. Spotted eagle rays are protected in Florida, USA but not in any other states in the USA or US federal waters, where they are not targeted. Fisheries targeting this species in Mexico and Cuba lack management plans for this ray and may be unsustainable.

Regulations such as closed fishing seasons, no-take zones, codes of conduct or regulations for tourism activities (WWF 2017) of the most popular sites during the spotted eagle ray season may be necessary. Spotted

eagle rays face many natural and anthropogenic threats, however, the scarcity of information on their ecology and movement patterns limits the accurate assessment of their conservation status and threats. Understanding the migration pathways and aggregation sites would be useful to sustain their populations throughout international waters. Thus, further monitoring using photo-ID across seasons and including areas outside the Mexican Caribbean is needed. Increasing efforts in Mexico, Cuba, other Caribbean nations and the USA will help in understanding long-term population trends and migration patterns of spotted eagle rays as well as their capacity to support targeted fisheries and tourism.

Acknowledgements We thank the dive operators, dive associates, and underwater photographers who contributed photographs and without whom this study would not have been possible. We also would like to thank Ivan Mendez Loeza, Breanna DeGroot and Dr. Matt Ajemian for training and constructive suggestions on the project's methods, as well as our collaborator Gabriela López Carrasco for photograph processing. We would like to thank Aquaworld, SCUBA Cancun and Solo Buceo for their ongoing assistance and field support. Funding and in-kind support for this project was provided by Disney Worldwide Conservation Fund, Save Our Seas Foundation, Mote Scientific Foundation and anonymous donors. This study was conducted in accordance with the Parque Nacional Arrecifes de Puerto Morelos regulations for conducting research in a national marine park (No. F00.9. DNAPM.422/15).

References

Ajemian M, Powers S (2014) Towed-float satellite telemetry tracks large-scale movement and habitat connectivity of myliobatid stingrays. *Environ Biol Fish* 97:1067–1081. <https://doi.org/10.1007/s10641-014-0296-x>

Ajemian MJ, Powers SP, Murdoch TJT (2012) Estimating the potential impacts of large mesopredators on benthic resources: integrative assessment of spotted eagle ray foraging ecology in Bermuda. *PLoS One* 7:e40227. <https://doi.org/10.1371/journal.pone.0040227>

Andrews KS, Levin PS, Katz SL, Farrer D, Gallucci VF, Bargmann G (2007) Acoustic monitoring of sixgill shark movements in Puget sound: evidence for localized movement. *Can J Zool* 85:1136–1143

Bassos-Hull K, Wilkinson K, Hull P, Dougherty D, Omori K, Ailloud L, Morris J, Hueter R (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>

Bonfil R, Meyer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Otze D, Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310:100–103

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Inst., Washington D.C

CONCANACO, SERVITUR (2016) Boletín Turismo. Confederación de Cámaras Nacionales de Comercio. Servicios y Turismo, México

Corcoran MJ, Gruber SH (1999) The use of photoidentification to study social organization of the spotted eagle ray, *Aetobatus narinari* (Euphrasen 1790), at Bimini, Bahamas: a preliminary report. *Bahamas J Sci* 7:21–27

Córdoba-Ordoñez J, García A (2003) Turismo, globalización y medio ambiente en el Caribe mexicano. *Investigaciones Geográficas, Boletín del Instituto de Geografía, UNAM* 52:117–136

Correa F, Manjarrés L (2004) Recursos de peces demersales explotados por las pesquerías artesanales marítimas de La Guajira, Caribe Colombiano. In: Manjarrés L (ed) *Pesquerías demersales del área norte de Colombia y parámetros biológico-pesqueros y poblacionales del recurso pargo* Univ. Magdalena, Santa Marta, Colombia, pp 77–91

Couturier LIE, Jaine FRA, Townsend KA, Weeks SJ, Richardson AJ, Bennett MB (2011) Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Kreffit, 1868), along the east coast of Australia. *Mar Freshw Res* 62:628–637. <https://doi.org/10.1071/MF10148>

Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ (2012) Biology, ecology and conservation of the Mobulidae. *J Fish Biol* 80:1075–1119. <https://doi.org/10.1111/j.1095-8649.2012.03264.x>

Cuevas-Zimbrón E, Pérez-Jiménez J, Méndez-Loeza I (2011) Spatial and seasonal variation in a target fishery for spotted eagle ray *Aetobatus narinari* in the southern Gulf of Mexico. *Fish Sci* 77: 723–730. <https://doi.org/10.1007/s12562-011-0389-9>

Davies TK, Stevens G, Meekan MG, Struve J, Rowcliffe JM (2012) Can citizen science monitor whale-shark aggregations? Investigating bias in mark-recapture modelling using identification photographs sourced from the public. *Wildl Res* 39:696–704. <https://doi.org/10.1071/WR12092>

den Hartog J, Reijns R (2007) Interactive Individual identification system (I3S). Version 2.0. www.reijns.com/i3s

Dewar H, Mous P, Domenier M, Muljadi A, Pet J, Whitty J (2008) Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Mar Biol* 151:121–133

DOF (2012) Diario Oficial de la Federación. Carta Nacional Pesquera. Publicada el Viernes 24 de Agosto de 2012. In: Ciudad de México

Dubick J (2000) Age and growth of the spotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790), from southwest Puerto. MSc thesis, University of Puerto Rico. p 79

Edney J (2006) Impacts of recreational SCUBA diving on shipwrecks in Australia and the Pacific, a review. *Micrones J Humanit Soc Sci* 5:201–233

Ellis JR, Morel G, Burt G, Bossy S (2011) Preliminary observations on the life history and movements of skates (Rajidae) around the Island of Jersey, western English Channel. *J Mar Biol Assoc UK* 91:1185–1192. <https://doi.org/10.1017/S0025315410001906>

Flowers KI, Ajemian MJ, Bassos-Hull K, Feldheim KA, Hueter RE, Papastamatiou YP, Chapman DD (2016) A review of batoid philopatry, with implications for future research and population management. *Mar Ecol Prog Ser* 562:251–261

- González-Ramos MS, Santos-Moreno A, Rosas-Alquicira EF, Fuentes-Mascorro G (2016) Validation of photo-identification as a mark–recapture method in the spotted eagle ray *Aetobatus narinari*. *J Fish Biol.* <https://doi.org/10.1111/jfb.13215>
- Iversen ES, Jory DE, Bannerot SP (1986) Predation on queen conchs, *Strombus gigas*, in the Bahamas. *Bull Mar Sci* 39: 61–75
- Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA (2009) Fidelity, homing and population structure revealed using electronic and genetic tag in white sharks of the Eastern Pacific. *Proc R Soc B Biol Sci* 1155:1–11. <https://doi.org/10.1098/rspb.2009.1155>
- Kitchen-Wheeler A-M (2010) Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. *Mar Biol Res* 6:351–363. <https://doi.org/10.1080/17451000903233763>
- Klimley A, Butler S (1988) Immigration and emigration of a pelagic fish assemblage to seamounts in the Gulf of California related to water mass movements using satellite imagery. *Mar Ecol Prog Ser* 49:11–20
- Kyne PM, Ishihara H, Dudley SFJ, White WT (2006) *Aetobatus narinari* IUCN 2013. IUCN red list of threatened species. Version 2013.1. www.iucnredlist.org
- Last PR, Stevens JD (2009) *Sharks and rays of Australia*, 2nd edn. CSIRO, Collingwood, Vic
- Lupton J (2009) The application of I3S Manta version 2.1 to the individual identification of white spotted eagle rays (*Aetobatus narinari*): A preliminary study
- Marshall AD (2008) Biology and population ecology of *Manta birostris* in southern Mozambique. Ph.D. thesis. In: The University of Queensland
- Marshall AD, Bennett MB (2010) Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *J Fish Biol* 77:169–190. <https://doi.org/10.1111/j.1095-8649.2010.02669.x>
- Marshall A, Dudgeon C, Bennett M (2011) Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Mar Biol* 158:1111–1124. <https://doi.org/10.1007/s00227-011-1634-6>
- Naylor GJP, Ryburn JA, Fedrigo O, Lopez A (2005) Phylogenetic relationships among the major lineages of modern elasmobranchs. In: Hamlett WC, Jamieson BGM (eds) *Reproductive biology and phylogeny*, vol 3. EnWeld, NH. Science Publishers, pp 1–25
- Randall JE (1964) Contributions to the biology of the queen conch, *Strombus Gigas*. *Bull Mar Sci* 14:246–295
- Richards VP, Henning M, Witzell W, Shivji MS (2009) Species delineation and evolutionary history of the globally distributed spotted eagle ray (*Aetobatus narinari*). *J Hered* 100: 273–283. <https://doi.org/10.1093/jhered/esp005>
- Schluessel V, Bennett MB, Collin SP (2010a) Diet and reproduction in the white-spotted eagle ray *Aetobatus narinari* from Queensland, Australia and the Penghu Islands, Taiwan. *Mar Freshw Res* 61:1278–1289. <https://doi.org/10.1071/MF09261>
- Schluessel V, Broderick D, Collin SP, Ovenden JR (2010b) Evidence for extensive population structure in the white-spotted eagle ray within the Indo-Pacific inferred from mitochondrial gene sequences. *J Zool* 281:46–55. <https://doi.org/10.1111/j.1469-7998.2009.00680.x>
- Sellas AB, Bassos-Hull K, Pérez-Jiménez JC, Angulo-Valdés JA, Bernal MA, Hueter RE (2015) Population structure and seasonal migration of the spotted eagle ray, *Aetobatus narinari*. *J Hered* 106:266–275. <https://doi.org/10.1093/jhered/esv011>
- Shepherd TD, Myers RA (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecol Lett* 8:1095–1104. <https://doi.org/10.1111/j.1461-0248.2005.00807.x>
- Silliman W, Gruber SH (1999) Behavioral biology of spotted eagle ray, *Aetobatus narinari*. *Bahamas J Sci* 7:13–20
- Tagliafico A, Rago N, Rangel S, Mendoza J (2012) Exploitation and reproduction of the spotted eagle ray (*Aetobatus narinari*) in the Los Frailes Archipelago, Venezuela. *Fish Bull* 110:307–316
- Van Tienhoven AM, Den Hartog JE, Reijns RA, Peddemors VM (2007) A computer-aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. *J Appl Ecol* 44:273–280. <https://doi.org/10.1111/j.1365-2664.2006.01273.x>
- Vaudo JJ, Lowe CG (2006) Movement patterns of the round stingray *Urolophus halleri* (Cooper) near a thermal outfall. *J Fish Biol* 68:1756–1766
- White WT, Last PR, Naylor GJP, Jensen K, Caira JN (2010) Clarification of *Aetobatus ocellatus* (Kuhl, 1823) as a valid species, and a comparison with *Aetobatus narinari* (Euphrasen, 1790) (Rajiformes: Myliobatidae). In: Last PR, White WT, Pogonoski JJ (eds) *Descriptions of new sharks and rays from Borneo*. CSIRO marine and atmospheric research, Hobart, pp 141–164
- White J, Simpfendorfer CA, Tobin AJ, Heupel MR (2014) Spatial ecology of shark-like batoids in a large coastal embayment. *Environ Biol Fish* 97:773–786. <https://doi.org/10.1007/s10641-013-0178-7>
- WWF (2017) *Responsible shark and ray tourism, a guide to best practice*. WWF, Project Aware, Manta Trust, p 87
- Yamaguchi A, Kawahar aI, Ito S (2005) Occurrence, growth and food of longheaded eagle ray, *Aetobatus flagellum*, in Ariake sound, Kyushu, Japan. *Environ Biol Fish* 74:229–238