GIANT MANTA RAY (*MOBULA BIROSTRIS*)

The giant manta ray is listed as a threatened species under the ESA (83 FR 2916, January 22, 2018). Critical habitat is not designated (84 FR 66652; December 5, 2019).

SPECIES DESCRIPTION

Physical Description of the Species

The giant manta ray has a diamond-shaped body with wing-like pectoral fins; the distance over this wingspan is termed disc width (DW). It may be the largest living ray species, attaining a maximum size of 800 cm DW, with anecdotal reports up to 910 cm DW (Compagno 1999; Alava et al., 2002; Carpenter et al., 2023). There are two distinct color types: chevron and black (melanistic). Most of the chevron variants have a black dorsal surface and a white ventral surface with distinct patterns on the underside that can be used to identify individuals (Marshall et al., 2008; Kitchen-Wheeler 2010; Deakos et al., 2011). While these markings are assumed to be permanent, there is some evidence that the pigmentation pattern of giant manta ray may actually change over the course of development (based on observation of two individuals in captivity), and thus caution may be warranted when using color markings for identification purposes in the wild (Ari 2015). The black color variants are entirely black on the dorsal side and almost completely black on the ventral side, except for areas between the gill-slits and the abdominal area below the gill-slits (Kitchen-Wheeler 2013). They also have distinct spot patterns on their bellies that can be used to identify individuals (Luiz et al., 2009; Kitchen-Wheeler, 2010; Couturier et al., 2011; Deakos et al., 2011; Marshall et al., 2011).

Habitat

The giant manta ray inhabits tropical, subtropical, and temperate bodies of water and is commonly found offshore, in oceanic waters, and near productive coastlines, with water temperatures generally between 20°C and 30°C (Duffy and Abbott 2003; Marshall et al., 2009; Kashiwagi et al., 2011; Freedman and Roy 2012; Graham et al., 2012; Hacohen-Domené et al., 2017; Farmer et al., 2022). Manta rays are commonly seen in surface waters or cleaning in shallow coral reef habitats typically in tropical or subtropical regions (Couturier et al., 2012; Braun et al., 2014). The giant manta ray can exhibit diel patterns in habitat use, moving inshore during the day to clean and socialize in shallow waters (10-20 m), and then moving offshore at night to feed to depths of 1,000 meters (Hearn et al. 2014; Burgess 2017). The coastal vertical movements of giant manta rays maybe motivated by a combined foraging and thermal recovery strategy, whereby giant manta rays dived to forage on vertically migrating zooplankton at night and returned to surface waters (<2 m) to rewarm between dives (Andrzejaczek et al., 2021). In coastal areas, giant manta rays have been observed in shallow waters, sometimes less than 3 meters deep, in estuarine waters, near coastal inlets, with use of these shallow waters as potential nursery habitats (Adams and Amesbury 1998; Milessi and Oddone 2003; Medeiros et al., 2015; Pate and Marshall 2020; Farmer et al., 2022).

Diet and Feeding

Giant manta rays primarily feed on planktonic organisms such as euphausiids, copepods, mysids, decapod larvae and shrimp, but some studies have noted their consumption of small and moderate sized fishes (Bertolini 1933; Bigelow and Schroeder 1953; Carpenter and Niem 2001; Rohner et al., 2017a; Stewart et al., 2017; Medeiros et al., 2022). While there are no studies that compare diet requirements for the different life stages, recent studies suggest that both juveniles and adults may occupy the same habitats within a location and, thus, target the same prey (Stewart et al., 2016b, Stewart et al., 2017, Graham et al., 2012). Manta rays have a complex depth profile of their foraging habitat (Andrzejaczek et al., 2021). Burgess et al., (2016) found that, on average, mesopelagic sources contributed 73% to the giant manta ray's diet, compared to 27% for surface zooplankton suggesting that giant manta rays may be supplementing their diet with opportunistic feeding in near-surface waters (Couturier et al., 2013; Burgess et al., 2016).

The feeding behaviors of manta species have also been studied to provide insight into their cognition and response to sensory stimuli. When feeding, groups of manta rays hold their cephalic fins in an "o" shape and open their mouths wide. They tend to swim at a speed around 30 pectoral fin beats per minute when feeding, which is almost twice as fast as they swim when being cleaned (Kitchen-Wheeler 2013). After collecting water with zooplankton in their mouths, manta rays use a transverse curtain on the roof of the mouth as a valve to hold the water in as the pharynx contracts during swallowing (Bigelow and Schroeder 1953). This movement of the pharynx pulls plankton towards the stomach when the gills are closed (Kitchen-Wheeler 2013). Intestinal eversion has also been observed, likely to clear the intestines of indigestible material and parasites (Clark and Papastamatiou 2008). The positioning of the cephalic fins was found to be a good indicator of feeding motivation, triggered by underwater visual stimuli or olfactory stimuli / sense of smell (Ari and Correia 2008).

LIFE HISTORY INFORMATION

Reproduction

The giant manta ray is ovoviviparous and is thought to produce a single offspring per pregnancy after a gestation period of 12-13 months (Rambahiniarison et al., 2018; Murakumo et al., 2020). An average female produces 4–7 pups during its lifespan (Marshall et al., 2022).

Age at Maturity

Males mature at 350–400 cm DW and females mature at 380–500 cm DW (White et al., 2006; Last et al., 2016; Stewart et al., 2018b). Female giant manta rays mature at 8.6 years of age, although first pregnancy may be delayed by up to 4 years depending on food availability (Rambahiniarison et al., 2018). Maximum age is estimated at 45 years and generation length is estimated to be between 20 years (J. Carlson unpublished) to 29 years (Marshall et al., 2022).

Habitat Use by Different Life Stages

Identifying potential manta ray important habitats, such as nursery, feeding and reproductive areas, especially in data limited regions such as the northwest Atlantic Ocean, is essential to conservation and recovery of this species. A recent study conducted off the Atlantic coast of central Florida provided evidence of reproductive habitat for manta rays (Pate 2024). Each spring, manta rays aggregate off the coast of central and northern Florida between Indian River County, Florida and the Florida/Georgia border. Pate (2024) documented numerous courtship and breaching events indicating that this area is potentially seasonal reproductive habitat for manta rays. This same study suggested that this area maybe important feeding habitat as feeding behaviors and prey species were also documented (Pate 2024). These initial observations warrant future study to determine the importance of this area to manta ray feeding and reproduction, as well as characterization of the environmental influences that affect manta ray presence and behavior.

Documenting juvenile nursery habitats is a priority in manta ray research and conservation (Stewart et al., 2018a), yet few have been described. Worldwide few nursery areas for manta rays have been described; however, two manta ray nursery habitats have been described in the

U.S Atlantic and Gulf of Mexico. Pate and Marshall (2020) described the nearshore area between St. Lucie Inlet and Boynton Beach Inlet in southeast Florida as nursery habitat for manta rays. Nearly all (98%) of manta rays observed by Pate and Marshall (2020) were juveniles and many showed high site fidelity to this nursery habitat. Observations of juvenile giant manta rays as far south as Miami suggest this nursery habitat may extend farther south (J. Pate, MMF, pers comm. to C. Horn, NMFS, June 4, 2024). As of December 2023, 151 juvenile manta rays had been identified within the nursery habitat, with 52% being re-sighted and 26% re-sighted over multiple years (Pate and Fong 2023). New individuals are being identified regularly along southeast Florida (J. Pate unpublished data). In addition, the Flower Garden Banks National Marine Sanctuary and the surrounding banks in the northwest Gulf of Mexico have been described as manta ray nursery habitat (Stewart et al., 2018a). These nursery habitats were described based on frequent observations of immature individuals in these areas, high site fidelity with individuals remaining in the areas, and extended use of these areas by individuals over multiple years (Heupel et al., 2017; Stewart et al 2018a; Pate and Marshall 2020).

Seasonal Distribution Patterns

In the U.S Atlantic, giant manta rays are distributed from Florida to as far north as New York, with a clear expansion to the north during warmer months. The highest nearshore occurrence is predicted to take place off the Atlantic coast of Florida during April, with the distribution extending northward along the shelf-edge as temperatures warm, leading to higher occurrences north of Cape Hatteras, North Carolina from June to October, and then south of Savannah, Georgia from November to March as temperatures cool (Figure 1; Farmer et al., 2022). These findings are consistent with other lines of evidence that demonstrate that large numbers of giant manta rays are known to migrate to the Atlantic coast of Florida during the spring and summer (Levesque 2019; Pate and Fong 2023). Aerial observations of manta ray movements indicate that the Atlantic coast of Florida is potentially an important foraging and reproductive habitat (Pate and Fong 2023; Pate 2024). Each spring manta rays aggregate off the coast of central and northern Florida, between Indian River County, Florida, and the Florida/Georgia border. Typically, individuals are observed during March of each year in coastal waters off Indian River County, then migrate northward, possibly coinciding with rising water temperatures. Anglers reported that when temperatures range between 68 and 72°F both manta ray and cobia abundance peaked, usually between March and April (Braun et al., 2024), which is consistent with findings in Farmer et al., (2022). Additionally, several lines of evidence indicate that the Mississippi delta region is an important aggregation. Farmer et al. (2022) predicted that the highest nearshore occurrence of giant manta rays in the Gulf of Mexico occurs around the Mississippi River Delta from April to June and again from October to November (Figure 1; Farmer et al., 2022). These findings are supported by directed research and survey efforts, public sightings, and fisheries bycatch data that indicate the Mississippi River Delta is likely an important aggregation site (NOAA 2024; NMFS, unpublished data).

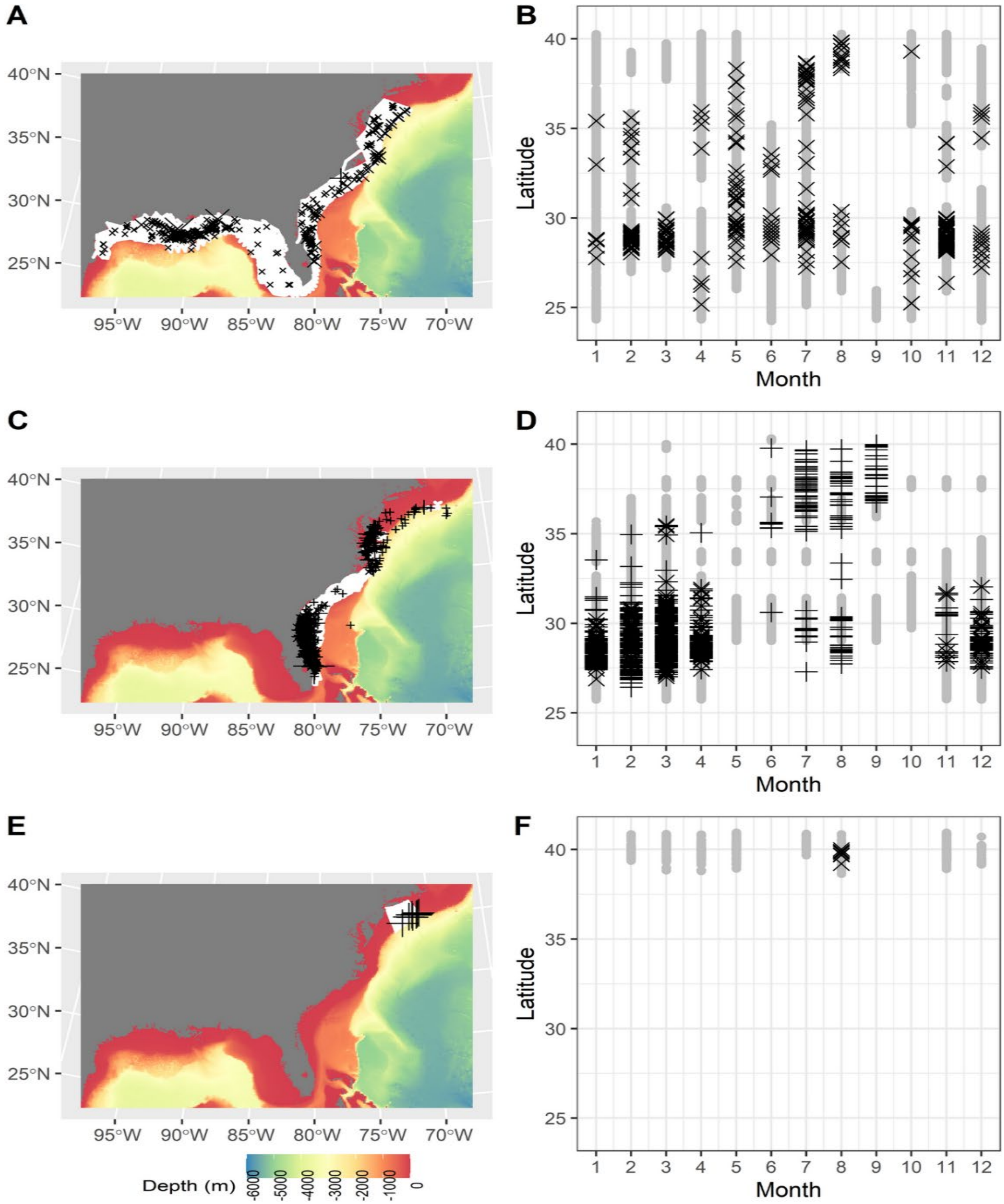

Figure 1: (A) Spatial distribution relative to coarse-scale bathymetry (red = shallow; blue = deep) and survey effort (white lines) and (B) spatio-temporal distribution of survey effort (gray circles) and manta ray sightings (X: on effort, + : off effort; scaled to number reported within survey) by Southeast Fisheries Science Center, (C,D) North Atlantic Right Whale Consortium, and (E,F) Normandeau Associates aerial surveys for New York State Energy Research and Development Authority. Source: Farmer et al., (2022).

Predators and Competitors

Manta rays are frequently sighted with non-fatal injuries consistent with shark attacks, although the prevalence of these sightings varies by location (Homma et al. 1999; Ebert 2003; Mourier 2012). Deakos et al. (2011) reported that scars from shark predation, mostly on the posterior part of the body or the wing tip, were evident in 24% of reef manta ray individuals (n=70 individuals with injuries) observed at a manta ray aggregation site off Maui, Hawaii. Off eastern Australia, Couturier et al. (2014) observed 23% of reef manta rays had shark scars. Approximately 76% of reef manta rays bear bite wounds of predatory sharks in southern Mozambique (Marshall & Bennett 2010a). Because the damage from a shark bite usually occurs in the posterior region of the manta ray, there may be disfigurement leading to difficult clasper insertion during mating or inhibited waste excretion (Clark and Papastamatiou 2008).

POPULATION DYNAMICS

Population Size

Although the global population size is not known, regional populations have been estimated in Ecuador, Indonesia, Mexico, and Mozambique. Ecuador's Machalilla National Park and the Galapagos Marine Reserve is thought to be home to the largest identified population of giant manta ray in the world, with the estimated population size of 11,022 (95% CI: 9095−13 357) for females and 11,294 (9456−13 490) for males (Hearn et al., 2014; Harty et al., 2022). The next largest population has been noted in Raja Ampat, Indonesia, but is much smaller, estimated at around 1,875 individuals (Beale et al., 2019). The other estimated populations are similar in size, with 1,172 individuals the Revillagigedo Archipelago, Mexico (Cabral et al., 2023), more than 400 individuals in Banderas Bay, Mexico (Domínguez-Sánchez et al., 2023), and 600 individuals Mozambique (Marshall 2008). Preliminary (uncorrected for availability bias) relative abundance estimates for giant manta rays in the northwest Atlantic Ocean and Gulf of Mexico, U.S., suggest an abundance ranging from approximately 5,000–14,000 individuals with a coefficient of variation between 14–20%, depending on the month (N. Farmer unpubl. data 2023). Preliminary satellite tagging returns from nine individuals suggest manta rays in the southeast spend a median of 14% of their time within depths visible to aerial observers; adjusted estimates for this availability bias suggest 47,802±121,032 (mean ± SD; range 8,206–161,804) individuals in the northwest Atlantic off the eastern U.S. (N. Farmer unpubl. data 2023). Locally, abundance varies substantially and may be based on food availability and the degree that they were, or are currently, being fished. In most regions throughout their range, the number of giant manta rays observed over the years appear to be small (fewer than 1,000 individuals) (NMFS 2024).

Population Variability

The trend of the number of individuals within populations varies widely across the species range, but trends appear stable where they are protected and declining rapidly where fishing pressure is greater (Marshall et al., 2022). For example, sighting trends appear stable where they receive some level of protections, such as Hawaii (Ward-Paige et al., 2013) and Ecuador (Holmberg and Marshall 2018), although individuals sighted in Ecuador seasonally migrate to Peru (A. Marshall unpubl. data 2019) where directed fishing occurs (Heinrichs et al., 2011). Elsewhere, the number of individuals is likely to be declining in places where the species is targeted or caught regularly as bycatch. For example, in southern Mozambique, a 94% decline in diver sighting records occurred over a 15-year period in a well-studied population (Rohner et al., 2017). Similarly, at Cocos Island, Costa Rica, there has been an 89% decline in diver sighting records of giant manta rays over a 21-year period (White et al., 2015). These steep declines have occurred in less than one-generation length (29 years) (Marshall et al., 2022). Although sparse, the available data suggest that target fisheries in some regions have rapidly depleted localized populations of the giant manta ray; local extinction is suspected to have occurred in many parts of their historical range. Globally, the suspected population reduction is 50–79% over three generation lengths, with a further population reduction suspected over the next several generations based on current and ongoing threats and exploitation levels, steep declines in monitored populations, and a reduction in area of occupancy (Marshall et al., 2022).

RANGE AND DISTRIBUTION

Within the Northern hemisphere, the giant manta ray has been documented as far north as the following locations: New York, U.S. and the Azores Islands in the Atlantic Ocean region; the Sinai Peninsula, Egypt in the Indian Ocean region; and Mutsu Bay, Aomori, Japan and southern California, U.S. in the Pacific Ocean region (Figure 2; Lawson et al., 2017; Kashiwagi et al., 2010; Moore 2012; CITES 2013; Sobral and Alfonso 2014; Knochel et al., 2022; Farmer et al., 2022). In the Southern Hemisphere, the species has been observed as far south as Peru in the eastern Pacific Ocean, Uruguay and St. Helena Island in the Atlantic Ocean, South Africa and

Australia in the Indian Ocean, and off Tasmania, New Zealand, and French Polynesia in the western and central Pacific Ocean (Figure 2; Lawson et al., 2017; Mourier 2012; CITES 2013, Couturier et al., 2015; Carpentier et al., 2019, Beard et al., 2021).

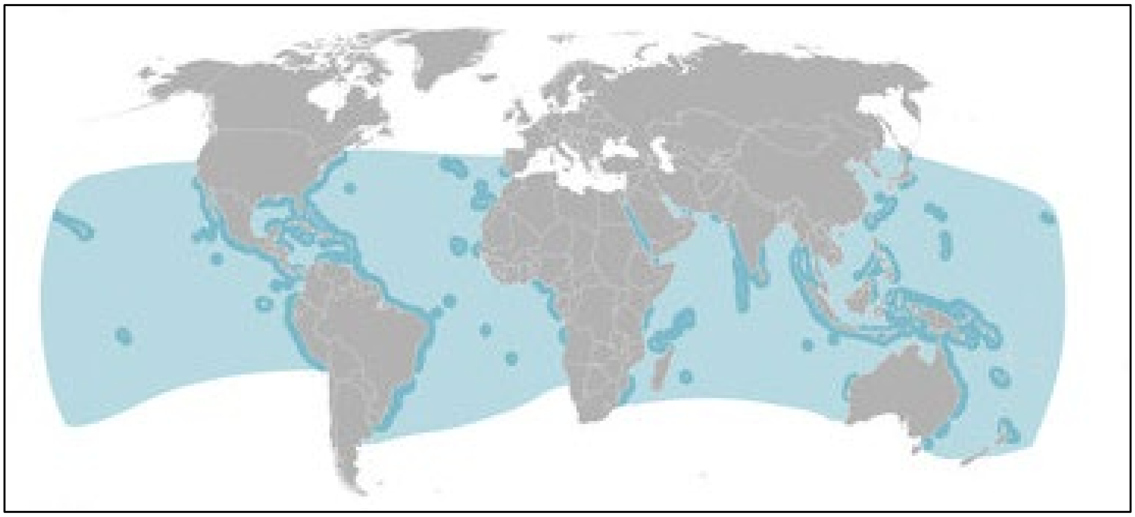

Figure 2: Geographic range of giant manta ray showing confirmed locations (extend in dark blue) as well as presumed range (possibly extant in light blue) (Lawson et al., 2017).

Biotic and Abiotic Factors Dictating Range / Distribution

Giant manta rays are commonly sighted in aggregations at many locations throughout their range, including: Similan Islands (Thailand); Raja Ampat (Indonesia); Sharm el-Sheikh (Egypt); Fuvahmulah and Addu Atolls (Maldives); northeast North Island (New Zealand), Kona, Hawaii (U.S.); U.S. Atlantic and Gulf of Mexico, Brazil; Cabo Verde; Isla de la Plata (Ecuador); Ogasawara Islands (Japan); Isla Margarita and Puerto la Cruz (Venezuela); northern coast of the Yucatan Peninsula; Isla Holbox; Revillagigedo Islands; and Bahia de Banderas (Mexico) (Notarbartolo-di-Sciara and Hillyer 1989; Homma et al., 1999; Duffy and Abbott 2003; Luiz et al., 2009; Clark 2010; Kashiwagi et al., 2010; Marshall et al., 2011a; Stewart et al., 2016a; Hacohen-Domené et al., 2017; Hilbourne and Stevens 2019; Pate 2024; Farmer et al., 2022; Knochel et al., 2022; Domínguez-Sánchez et al., 2023; Garzon et al., 2023). The timing of these aggregations varies by region and seem to correspond with the movement of zooplankton, climatic fluctuations (e.g., El Niño Southern Oscillation), current circulation and tidal patterns, seasonal upwelling, seawater temperature, and possibly mating behavior (Couturier et al., 2012; De Boer et al., 2015; Armstrong et al., 2016; Hacohen-Domené et al., 2017; Beale et al., 2019; Nicholson-Jack et al., 2021; Domínguez-Sánchez et al., 2023, Garzon et al., 2023). For example, in the U.S. Atlantic and Gulf of Mexico, the distribution of manta rays was found to be influenced primarily by sea surface temperature, with a clear expansion to the north during warmer months (Farmer et al., 2022). Additionally, within the preferred thermal range (approximately 68–86°F), manta rays occurred most frequently either nearshore or along the continental shelf-edge, at locations best predicted by proxies for productivity such as thermal fronts, bathymetric slope, and high chlorophyll-a concentration (Farmer et al., 2022).

THREATS

Past and Current Threats Resulting in Population Declines

The largest cause of direct mortality of giant manta rays globally is targeted fishing and capture as bycatch (Croll et al., 2016; NMFS 2024), though they face a range of other threats including marine pollution, vessel strikes, and entanglement (NMFS 2024). In addition, while there is no direct evidence, there is concern for this species as a result of impacts associated with climate change (Essumang 2010, Ooi et al., 2015, Stewart et al., 2018).

Fisheries (Foreign)

Giant mana rays are both targeted and caught incidentally in industrial and artisanal fisheries (Couturier et al., 2012; Croll et al., 2016; Stewart et al., 2018). These rays are captured in a wide range of gear types including harpoons, drift nets, purse seine nets, gill nets, traps, trawls, and longlines. Their coastal and offshore distribution, and tendency to aggregate, makes giant manta rays particularly susceptible to bycatch in purse seine and longline fisheries and targeted capture in artisanal fisheries (Croll et al. 2016; Duffy and Griffiths 2017). In particular, giant manta rays are easy to target because of their large size, slow cruising speed, tendency to aggregate, predictable habitat use, and lack of human avoidance (Couturier et al., 2012). Manta ray catches have been recorded in at least 30 large and small-scale fisheries covering 25 countries (Lawson et al., 2016). The largest documented target fisheries are Indonesia, the Philippines, and India (NMFS 2024). While many artisanal fisheries have grown to meet international trade demand for gill plates as discussed below, some still target these manta rays mainly for food and local products (White et al., 2006, Essumang 2010, Rohner et al., 2017).

Federal Fisheries (Southeast U.S.)

The giant manta ray is caught as bycatch in a number of federally-managed U.S. commercial fisheries operating in the Atlantic Ocean and Gulf of Mexico. Data comes from limited fisheries observer programs. Information was severely lacking on catch and fishing effort of the species in the Atlantic at the time of listing because rays were not identified to species in observer programs. In 2019, fisheries observer programs in the Southeast began identifying and recording bycatch for the giant manta ray, thus providing a better understanding of U.S. commercial fisheries interactions with giant manta rays. Based on all available observer data, the Southeast U.S. commercial fisheries that use trawls, pelagic and bottom longlines, gillnet, and hook and line gears occasionally incidentally capture giant manta rays. Shrimp trawl and pelagic longline gears appear to interact with giant manta rays the most, followed by bottom longline, and gillnet. Dispositions of the giant manta rays are recorded at the vessel (i.e., released alive, discarded dead, or disposition unknown) and the poor physical condition of some animals at upon release indicate that animals do die after these encounters. However, post-release mortality is unknown.

The Southeast Shrimp Trawl Fishery

The southeast U.S. shrimp fishery operates in the EEZ in the Gulf of Mexico and U.S. Atlantic, and observer coverage in this fishery is less than 2%. On April 26, 2021, the NMFS Southeast Regional Office (SERO) issued a Biological Opinion (Opinion) on the implementation of the sea turtle conservation regulations under the ESA for shrimp trawls and the authorization of the southeast U.S. shrimp fisheries in federal waters under the Magnuson-Stevens Act (NMFS 2021). As part of the Opinion, an incidental take statement was issued that anticipated the non-lethal capture of 16,780 giant manta rays over 10 years (averaging 1,678 giant manta rays per year) in the shrimp trawl fishery. No giant manta ray mortalities were anticipated because there were no records of lethal interactions at that time. The incidental take estimate was based on 1 year of data, which included 12 non-lethal interactions documented during that time, and was highly uncertain (Carlson 2020).

In 2023, NMFS reinitiated this consultation because there were giant manta ray mortalities documented by the observer program. Between 2019 and April 2024, the SEFSC shrimp observer program observed approximately 37 giant manta rays were incidentally captured, with 26 released alive, 4 dead, and 7 discarded with an “unknown” disposition (NMFS unpublished data). The majority of interactions were recorded off the coast of Louisiana, followed by coastal areas near the Florida/Georgia border. The lack of many interactions observed in the U.S Atlantic may be due to very low observer coverage, as several recent studies indicate that north and central Florida is likely an important habitat for giant manta ray migration, foraging and reproduction (Farmer et al., 2022; Pate 2024). The majority of interactions have occurred in Federal waters, although there are records in State waters as well.

The Pelagic Longline Fishery

The Pelagic Longline Fishery for Atlantic Highly Migratory Species comprises relatively distinct segments including: Caribbean, Gulf of Mexico, Florida east coast, South Atlantic bight, mid-Atlantic bight, northeast coastal Atlantic, northeast distant waters, Sargasso Sea, and Offshore waters. Observer coverage is maintained at a minimum of 8%, but some years have higher coverage (NMFS 2020).

On May 15, 2020, NMFS SERO issued an Opinion on the operation of the Pelagic Longline Fishery for Atlantic Highly Migratory Species in federal waters under the Magnuson-Stevens Act (NMFS 2020). As part of the Opinion, an incidental take statement was issued that anticipated the non-lethal capture of 366 giant manta rays and 6 mortalities over 3 years in the Pelagic Longline Fishery. At that time, the incidental take estimate was uncertain as there was limited incidental capture data of giant manta rays, including mortality data. In addition, uncertainty surrounded species identifications made by the observers as most records pre-dated the ESA listing of giant manta rays and subsequent observer training. In 2022, the NMFS reinitiated the consultation because the number of mortalities documented by the observers have exceeded what was authorized in the 2020 Opinion. From 2020 through 2023, observers (9.9% coverage) recorded 9 giant manta rays captured in pelagic longline gear, with 3 documented at-vessel mortalities. These captures occurred in the mid-Atlantic bight, northeast coastal Atlantic, and Gulf of Mexico fishing zones. Of note, the majority (approximately 71%) of mobulid bycatch records from 2019–2023 lacked identification to the species level; it is unclear what percentage of these records were comprised of giant manta ray.

The Coastal Migratory Pelagic Fishery

The Coastal Migratory Pelagic (CMP) Fishery operates in the Atlantic Ocean and Gulf of Mexico. The fishery primarily targets king mackerel, Spanish mackerel, and the Gulf of Mexico Migratory Group of cobia. The main gear types used in the CMP fishery are hook-and-line (primarily trolling), cast net, and gillnet. Diver-held spear guns are also a main gear type specific to cobia. Interactions with manta rays were observed in 2018 for commercial gillnet sets targeting Spanish mackerel. No interactions with giant manta rays for the gill net component of the king mackerel fishery were reported or observed (NMFS 2023). In addition, recreational anglers targeting cobia along Florida's east coast are known to track giant manta ray migrations for the purpose of targeting cobia (Pate 2023; Braun et al., 2024). These anglers will seek out and cast at or near giant manta rays to catch the cobia that are associated with the manta rays (e.g., cobia travel beneath manta rays) (Bishop, 1999; McNally, 2012; Roberts, 2022). This fishing practice primary occurs off Florida's east coast within the boundaries of the Gulf of Mexico Cobia Migratory Group within the Florida East Coast Zone.

On May 1, 2023, NMFS SERO issued an amendment to Biological Opinion on the operation of the CMP Fishery in federal waters under the Magnuson-Stevens Act (NMFS 2023). As part of the Opinion, an incidental take statement was issued that anticipated the non-lethal capture of 714 giant manta rays and 63 mortalities (including post-release mortality) over 3 years in the CMP Fishery. The incidental take is highly uncertain and is based on discard logbook and observer program data from 2010 to 2020. The discards have percent standard error values over 100 indicating a high level of uncertainty (NMFS 2023). A recent study that was published after the 2023 amendment to the CMP Biological Opinion (Braun et al., 2024), found 86% of cobia anglers interviewed along Florida's east coast reported that they had or their clients (charters) had incidentally hooked giant manta rays while casting at manta rays when fishing for cobia (Braun et al., 2024). In addition, 93% of anglers reported having observed giant manta rays with hooks and training lines or evidence of vessel strike injuries. Overcrowding and increased vessel activity is also a vessel strike concern as anglers have reported seeing an average maximum of 22 boats (range: 1–50) surrounding a single ray or group of rays at the same time (Braun et al., 2024). The most recent information indicates that this fishing practice results in a potentially significant amount of incidental hooking and an increased risk of vessel strike. It is also possible that vessel overcrowding and incidental hooking are disrupting giant manta rays use of this area which is used during migration and is a potentially important foraging and reproductive habitat for this species (Pate 2024).

Atlantic HMS Fisheries (Excluding the HMS Pelagic Longline Fishery)

Fisheries managed under the Consolidated Atlantic HMS FMP (excluding the pelagic longline fishery) operate within Federal waters of the U.S. EEZ. The gear types authorized include bandit gear, bottom longline, buoy gear, gillnets, green-stick, handline, harpoon, purse seine, rod and reel, and speargun. Giant manta rays have been recorded as catch in shark bottom longline gear, in the research fishery. The shark bottom longline research fishery has 100 percent observer coverage. Between 2008 and 2016, there were 2 giant manta rays reported caught in the shark bottom longline research fishery. In addition, Kroetz et al. (2020) reviewed observer data from 1998 to 2017 and documented giant manta ray interactions in drift gillnets (80%, n=6) targeting sharks. All these interactions occurred in the U.S. Atlantic, with the majority occurring along Florida's east coast, followed by nearshore North Carolina (Kroetz et al., 2020). Of the 6 observed interactions, one resulted in a mortality. As part of the Opinion, an incidental take statement was issued that anticipated the non-lethal capture of 9 giant manta rays over 3 years in the Consolidated Atlantic HMS Fishery.

STATE FISHERIES

Various fishing methods used in state commercial and recreational fisheries, including purse seine, gillnets, trawls, pot fisheries, and vertical lines are all known to incidentally take giant manta rays, but information on these fisheries and their impacts on giant manta rays is sparse (NMFS 2024). Most of the state fisheries data are based on extremely low observer coverage, if any, or giant manta rays were not part of data collection; thus, these data provide insight into gear interactions that could occur but are not indicative of the magnitude of the overall problem of fishery bycatch is state fisheries.

Secondary Threats

The largest cause of direct mortality of giant manta rays globally is targeted fishing and capture as bycatch, they face a range of secondary threats including: recreational fishing; vessel strikes; interactions; entanglement; oil spills; marine pollution; and climate change (NMFS 2024). While these threats are known, the extent to which these impacts may affect individual health and overall population fitness is unclear (Couturier et al., 2012; Croll et al., 2016; Stewart et al., 2018).

Recreational Fishing

Recreational fishing from private vessels and fishing piers may interact with giant manta rays. For example, giant manta rays have been observed and reported foul-hooked from boats, fishing piers, jetties, and by recreational anglers fishing for sharks during tournaments. Pate and Marshall (2020) found that 27% of the observed giant manta rays in southeast Florida were foul-hooked or entangled in fishing line, and, of those, 38% interacted with fishing gear more than once. More recent data found that of 152 individual manta rays recorded in southeast Florida, 23.7% had interactions with recreational fishing gear and, of those, 61% had multiple interactions (C. Horn., NMFS, pers comm to J. Pate, 2023). These manta rays were commonly seen in the vicinity of fishing piers and inlet jetties (Pate and Marshall, 2020), and anglers have been observed casting at juvenile manta rays (J.H. Pate unpublished data). NMFS has also documented several manta ray captures by anglers targeting sharks from the shore and from vessels (C. Horn unpubl. data). While some fishing interactions may result in minimal permanent injury to the manta ray, they likely cause considerable stress and possible sub-lethal effects. When fishermen have accidentally hooked manta rays, fight times have been over one hour (J. Pate unpubl. data cited in Pate and Marshall, 2020). Fight time is correlated with physiological stress (i.e., lactate production) in elasmobranchs, with smaller sharks producing more lactate than larger sharks (Gallagher et al. 2014). Fishing line entanglement can have non-lethal effects, including truncated cephalic fins (Deakos et al., 2011), deep lacerations to the body (Pate and Marshall 2020), stress (Gallagher et al., 2014), and impaired feeding or swimming. In addition, amputations and disfigurements, specifically those of the cephalic fin, may reduce feeding efficiency, and the absence of this fin may negatively affect size, growth rate and reproductive success (Marshall and Bennett 2010, Deakos et al., 2011, Couturier et al., 2012, Stewart et al., 2018a). While there have been no manta ray deaths directly attributed to recreational fishing, mortality may be cryptic as manta rays are negatively buoyant, reducing the likelihood of dead animals washing ashore.

Vessel Strike

Vessel strikes are evident in every monitored manta ray population across the globe (Stewart et al., 2018a). Spending considerable time at the surface (e.g., while feeding and basking; Braun et al., 2014; Braun et al., 2015) manta rays are especially susceptible to vessel strikes (McGregor et al., 2019; Stevens and Froman 2019; Armstrong et al., 2020; Augliere, 2020). Vessel strikes are spatially variable and are more likely to occur where vessel density and manta ray aggregation along surface waters is high. For example, off the Ningaloo Coast, vessel strikes were highest during the seasonal aggregation of manta rays, which was attributed to an abundance of zooplankton around the area (McGregor et al., 2019). In French Polynesia, observations of manta rays with sub-lethal injuries caused by fishing gear or boat strikes are more likely near inhabited islands than near uninhabited islands (Carpentier et al., 2019). In addition, in some parts of their range, such as the northwest Atlantic, it is likely that the seasonal contraction of suitable manta ray habitat during the warmer months increases their proximity to busy ports, which could pose a serious threat to the species (Garzon et al., 2020). For example, Garzon et al. (2020) found that the Southeast U.S., followed by Venezuela and The Bahamas, had the largest areas of overlap between predicted core manta ray habitat areas and intense commercial vessel traffic (Figure 3).

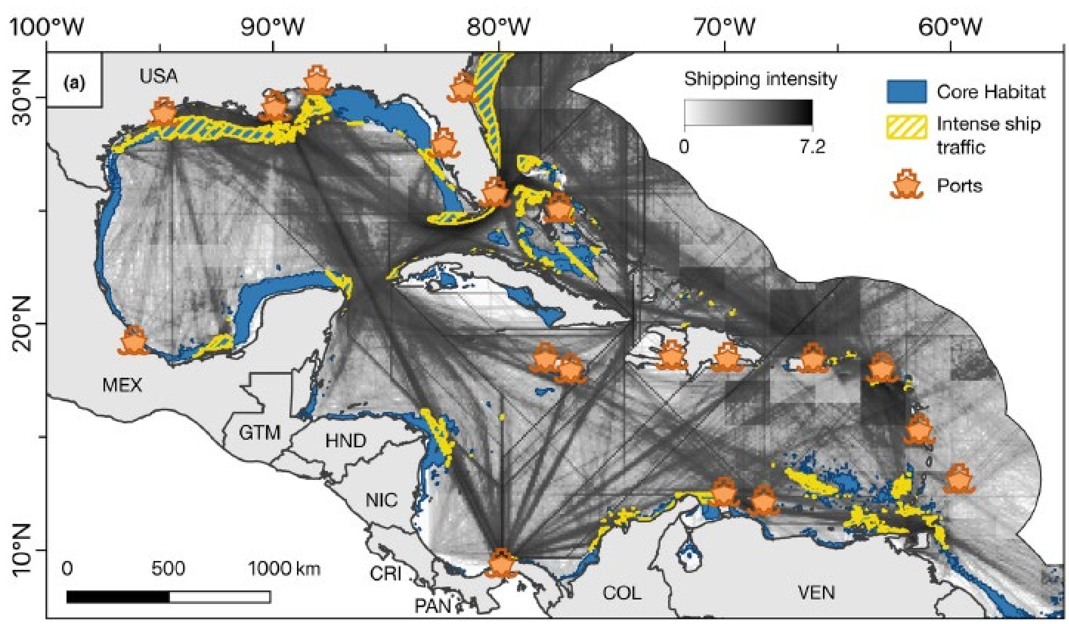

Figure 3: Core manta ray habitat predicted through ensemble ecological niche models with ship traffic, shipping routes and major ports displayed across the western central Atlantic. Source: Garzon et al. (2020)

When comparing the likelihood of vessel strikes on juveniles versus adults, the observed habitat use of juveniles may make them more prone to this threat (Strikes et al., 2022). For example, human activity and vessel traffic is extremely high in the giant manta ray nursery habitat along Florida's Atlantic coast, and vessel strikes are one of the most common sources of injuries to juvenile giant manta rays that frequent the coastal waters there (Pate and Marshall, 2020). Of the known individual giant manta rays (n=179) occurring in southeast Florida, 15 individuals (8.4%) have been recorded with apparently non-lethal vessel strike injuries between June 2016 and December 2023 (J. Pate, pers. comm. to C. Horn, NMFS SERO PRD, January 12, 2024). However, interpreting reported vessel strike data can be difficult due to the fact that many vessel strikes are not detected and/or go unreported, and there are reporting biases related to spatial coverage of reports (Pate and Marshall 2022; Garzon et al., 2020; McGregor et al., 2019). One source of underreporting for manta ray vessel strikes is the rapid wound healing characteristic of the species. McGregor et al. (2019) found that manta ray wound healing follows a negative exponential curve, with 37% of the wound closed after 33 days and 95% of the wound closed after 295 days making vessel strike injuries less likely to be identified the longer the wound goes unobserved. Further, researchers note that identifying vessel strike injuries once the wound is mostly closed is exceedingly difficult, especially when most photographs are poor quality making it difficult to observe the injury (C. Horn, NMFS pers comm. to J. Pate, MMF, July 18, 2024).

No information is currently available to estimate mortality rates for giant manta rays from vessel strikes. However, for sea turtles, greater than 75% of vessel strikes result in mortality with only 10-20% of vessel strikes being observed (Foley et al., 2019). The mortality rate for giant manta rays is likely higher because the giant manta ray's head and body cavity, which includes all major organs, is large, making up about approximately half of their body's surface area. While surface feeding and basking their body cavity and head are at the surface, unlike sea turtles, the giant manta ray has no hard shell to protect their vital organs, thus, making it more likely that injuries sustained to the head and body will be fatal. It is notable that all the vessel strike injuries documented within the southeast Florida survey domain have occurred on the individual's pectoral fins, not the head or body. Lethal vessel strikes are unlikely to be observed because giant manta rays sink once they die due to their lack of a swim bladder. For these reasons, the giant manta ray mortality rate and unobserved vessel strike death rate may be higher than sea turtles.

Entanglement in Non-fishing lines

The giant manta ray must constantly swim in order to move water over their gills to breathe, and mooring line or rope entanglement can significantly restrict their ability to swim, rapidly leading to asphyxiation and death (Manta Trust 2019). Entanglement in mooring, anchor line, ropes, and buoy lines can also cause disfigurements and amputations (i.e., missing cephalic lobes) (Braun et al., 2015; Convention on Migratory Species 2014; Couturier et al., 2012; Deakos et al., 2011; Germanov and Marshall 2014; Heinrichs et al., 2011). The eyes on a giant manta ray are positioned on the sides of their heads, limiting their vision in front of them. This makes it less likely that they will see a line directly in front of them as they swim forward. It is likely that giant manta rays become entangled because, when the line makes contact with the front of the head between the cephalic lobes, the animal's reflex response is to close the cephalic lobes, thereby trapping the rope, which entangles the animal as it begins to roll in an attempt to free itself (A. Marshall pers comm to C. Horn, NMFS, 2019). In 2017, a giant manta ray was documented as dead, entangled in a vessel exclusion line (steel cable) near Pompano Beach, Florida. The female measured 2.48 m in disc width and had no other signs of injury or fishing line entanglement. It is likely that the manta ray became entangled in the line and drowned (Pate et al., 2020). In Hawaii, numerous manta rays have been reported to have died or have evidence of injury (i.e., amputations or disfigurements) as a result of entanglement in mooring lines (Deakos, 2011). Mooring line entanglements have resulted in the death of numerous manta rays in the Maldives (Manta Trust, 2019). There have been several reported incidences of giant manta ray entanglements on vertical lines deployed during oil and gas activities. Oil and gas activities can deploy numerous vertical lines during operation including diver downlines, acoustic buoy release lines, acoustic pinger lanyards, nodal tether cables, and nodal lanyards etc. Similar to mooring line entanglements discussed above, the giant manta ray cannot see a vertical line directly in front of them and they become entangled once the line makes contact with their head. There have been several confirmed reports of giant manta rays becoming entangled in vertical lines deployed by commercial oil and gas divers in the Gulf of Mexico in recent years (C. Horn and N. Famer unpublished data 2022). For example, in 2013, 2021, and 2022, there were reports of giant manta rays entangled in a vertical downlines deployed by oil and gas divers. In addition, commercial oil and gas divers have reported numerous incidences of large rays, possibly giant manta rays in close proximity to underwater operations. It is thought that zooplankton are attracted to the underwater lights deployed by commercial divers. The amassing of zooplankton may be attracting giant manta rays to underwater operation sites where vertical lines are deployed increasing the risk of entanglement (C. Horn, NMFS, personal observation).

Marine Pollution

In locations with high densities of plastic debris and microplastics, giant manta rays may directly ingest plastic marine debris and microplastics, the consequences of which may include exposure to toxic plastic additives and persistent organic pollutants (POPs) (Stewart et al., 2018; Germanov et al., 2019). Studies have found elevated levels of some heavy metals in ray tissues (Essumang, 2009, 2010; Ooi et al., 2015) and low levels POPs (Germanov et al., 2019). Phthalates and/or POPs have been recorded in tissue samples of baleen whales, basking sharks, whale sharks, and manta rays in areas with high levels of microplastic pollution (Fossi et al., 2014, 2016, 2017; Germanov et al., 2019), indicating that filter feeding organisms are likely bioaccumulating these pollutants as a result of plastic ingestion. A number of studies have demonstrated that ingesting indigestible particles (e.g., microplastics) can block adequate nutrient absorption and cause damage to the digestive tract. Microplastics can also have high levels of toxins and POPs, and introduce these toxins to the animals via ingestion (Jakimska et al., 201; Germanov et al., 2018). These toxins can bioaccumulation over decades, in long-lived filer feeders like the giant manta rays, leading to potentially disruption of biological processes (i.e., endocrine disruption) and potentially altering reproductive fitness (Rochman, 2013; Rochman et al., 2014). Furthermore toxins can be transferred from mother to offspring (Lyons et al. 2013), potentially impacting growth survival and reproduction of progeny (Galloway and Lewis, 2016; Germanov et al., 2018). Additionally, zooplankton can be contaminated with pollutants and toxins (Fossi et al., 2014) through ingesting microplastics and nanoplastics (Cole et al., 2013; Setälä et al., 2014). This suggests that giant manta rays may be secondary consumers of microplastics and associated pollutants even if they are foraging in locations (or at depths) that do not have high densities of floating microplastics Yet, the implications of exposure to pollution and contaminants on the giant manta ray, remain speculative, especially at the level of individual fitness and population viability (Stewart et al., 2018).

Oil and Gas Activities

A recent ecological vulnerability assessment of elasmobranchs and other large pelagic fish found that giant manta rays have the highest ecological vulnerability (compared to other elasmobranch species) to oil spills within the Gulf of Mexico (Romo-Curiel et al., 2022). Giant manta rays are highly susceptible to the negative health effects associated with oil exposure because they are filter feeders that form seasonal aggregations near oil and gas infrastructure in the Gulf of Mexico (Carpenter, 2002; De la Parra Venegas et al., 2011; Couturier et al., 2012; Hueter et al., 2013; Worm et al., 2017; Germanov et al., 2018; Stewart et al., 2018; Kahane-Rabbort et al., 2022). Giant manta rays can also encounter oil while swimming, resting, basking, and feeding in their habitats impacted by oil spills. Because giant manta rays are negatively buoyant, carcasses will sink, suggesting a low probability of observing lethal oil impacts to the species. Direct contact with oil can result in significant health effects and jeopardize the giant manta ray's survival. The effects of ingesting indigestible particles, such as oil, include blocking adequate nutrient absorption and causing mechanical damage to the digestive tract. The giant manta ray may also ingest toxins through their prey since zooplankton can be contaminated with oil and other toxins (Fossi et al., 2014; Cole et al., 2013; Setälä et al., 2014; Goswami et al., 2023) causing significant health implications. While studies have suggested that highly mobile fish, like the giant manta ray, may actively shift habitat to avoid oil, thereby reducing or minimizing exposure, this active avoidance may alter important behavior (i.e., foraging and reproduction) and migration patterns, resulting in detrimental effects on populations (Pulster et al., 2020; Dornberger et al., 2020; Romo-Curiel et al., 2022).

Climate Change

Warming oceans cause changes in ocean acidity, oxygen content, oceanic circulation, and primary productivity dynamics, ultimately affecting food web structure and the distribution and availability of manta ray prey (Moloney et al., 2011). The major impact of climate change on manta rays is likely to be the projected decline in zooplankton biomass in tropical waters (Stewart et al., 2018a). Biogeochemical models predict that between 1980 and 2100 global zooplankton biomass will have declined by 7-16% (Chust et al., 2014; Stock et al., 2014; Woodworth-Jefcoats et al., 2017; Heneghan et al., 2023), but some regions, particularly those in the tropics, could experience >50% decline in zooplankton biomass (Stock et al., 2014). While it is unknown how this broad-scale decline in zooplankton biomass at the tropics could impact local areas where giant manta rays feed, the most likely outcome is that there will be lower zooplankton biomass available for manta rays. In addition, changes in climate and oceanographic conditions, such as acidification, are also known to affect zooplankton structure (size, composition, and diversity), phenology, and distribution (Guinder and Molinero 2013). As such, the migration paths and locations of both resident and seasonal aggregations of manta rays, which depend on these animals for food, may similarly be altered (Australian Government 2012; Couturier et al., 2012). To date, warming in northern latitudes off the US East Coast appears to have resulted in a significant northerly shift of manta ray distribution (Farmer et al., 2022). Resulting changes in zooplankton availability could affect the behavior and health of giant manta ray populations. For example, shifts in seasonal migration patterns to feeding grounds and nursery areas could have profound impacts on the species' survival. Additionally, some giant manta rays use coral reefs as cleaning stations where small fish remove parasites and dead or diseased skin from their bodies. As sensitive reef habitats degrade due to climate-driven changes, the abundance of cleaning stations and cleaner fish may be reduced (Jones et al., 2004; Graham et al., 2008). The loss of cleaning opportunities can hinder the giant manta ray's ability to reduce parasitic loads and dead tissue, leading to increased disease and reduced survival.

Aquarium Trade

The giant manta ray is traded internationally for display in public aquariums around the globe. Yet, there is limited information available on the number of animals taken from wild populations for the aquarium trade. Several known aquariums display manta rays collected from wild populations for public display. These aquariums include the Georgia Aquarium (United States), Okinawa Churaumi Aquarium (Japan), Nausicaá National Sea Center (France), Atlantis Resort (The Bahamas), S.E.A Aquarium (Singapore), and uShaka Marine World (Durban, South Africa). The available information indicates that some manta rays are transferred among aquariums. For example, the manta ray at UShaka Marine World outgrew its tank, and was eventually transferred to the Georgia Aquarium (Banks 2008). While most wild collected individuals remain in captivity, the Atlantis Resort is one facility that has successfully returned 13 individuals to the wild populations (Rutger 2018). There is limited information available on the total number of individuals collected for exhibition/aquarium purposes and whether those individuals are giant manta rays or reef manta rays. The only international trade data available comes from the CITES Trade Database. Since the giant manta ray was listed under Appendix II in 2016, the CITES Trade Database (https://trade.cites.org/) reports that two giant manta ray export permits were issued, both in 2018, for France to receive two giant manta rays from the United States for exhibition purposes.

With respect to domestic trade, Florida is the only state within the U.S. that authorizes giant manta ray collection for aquarium and exhibition purposes. The Florida Fish and Wildlife Conservation Commission (FWC) authorizes the collection of giant manta ray from the wild under a Special Activity License (SAL) for exhibition purposes. In 2009 and 2010, three giant manta rays were removed from Florida's waters for exhibition purposes for the Georgia Aquarium. More recently, from 2019 to 2022, the FWC has issued 17 SALs for the collection of giant manta rays for exhibition purposes. These SALs were issued to a number of aquarium facilities that were not previously known to exhibit/display manta rays, including: Nausicaá National Sea Center (France), Hainan Ocean Paradise (Hainan, China), Rizhao Ocean Park (Shandog, China), Changxing Taihu Longzhimeng Sea World (Shanghai, China), Chongqing Andover Ocean Park (Chongqing, China), SeaWorld Abu Dhabi (United Arab Emirates), and The National Aquarium LLC (Maryland, United States) (L. Gregg pers comm to C.Horn July 18, 2023). Despite the receiving the SALs, these facilities were not successful in collecting any individuals from Florida waters. In addition, no CITES export permits were issued for the collection licensed by the FWC. The FWC sets its annual collection quota based on the traditional level of collection request that the state has received for exhibition purposes (L. Gregg pers com to C. Horn, July 18, 2023).

REFERENCES

Acebes, J.M.V. and Tull, M. 2016. The history and characteristics of the mobulid ray fishery in the Bohol Sea, Philippines. PLOS ONE 11(8): e016144.

Adams, D. H., and E. Amesbury. 1998. Occurrence of the manta ray, Manta birostris, in the Indian River Lagoon, Florida. Florida Scientist 61(1):7-9.

Alava, M.N.R., Dolumbaló, E.R.Z., Yaptinchay, A.A. and Trono, R.B. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. Pp. 132-148. In: S.L. Fowler, T.M. Reed and F.A. Dipper (eds), Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop. Sabah, Malaysia, July 1997. Occasional paper of the IUCN Species Survival Commission No. 25.

Andrzejaczek, S., Schallert, R.J., Forsberg, K., Arnoldi, N.S., Cabanillas-Torpoco, M., Purizaca, W. and Block, B.A., 2021. Reverse diel vertical movements of oceanic manta rays off the northern coast of Peru and implications for conservation. Ecological Solutions and Evidence, 2(1), p.e12051.

Barnes, R.H. 2005. Indigenous use and management of Whales and other Marine Resources in East Flores and Lembata, Indonesia. Indigenous Use and Management of Marine Resources

Beale, C., Stewart, J., Setyawan, E., Sianipar, A., Erdmann, M.V. 2019. Population dynamics of oceanic manta rays (Mobula birostris) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño–Southern Oscillation on their movement ecology. Diversity and Distributions. 25. 10.1111/ddi.12962.

Bertrand A, Vögler Santos R, Defeo O. 2018.Climate change impacts, vulnerabilities and adaptations: Southwest Atlantic and Southeast Pacific marine fisheries. In: Barange M, Bahri T, Beveridge MCM, Cochrane KL, Funge-Smith S, Poulain F (eds) Impacts of climate change on fisheries and aquaculture: synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries and Aquaculture Technical Paper No. 627. Rome, FAO:325–346.

Bianchi, G. 1985. Field guide to the commercial marine and brackish water species of Tanzania. FAO Species Identification Sheets for Fishery Purposes. Project No. TCP/URT/4406. FAO, Rome.

Brainard, R. E., and coauthors. 2011. Status review report of 82 candidate coral species petitioned under the U.S. Endangered Species Act. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, NOAA Technical Memorandum NMFS-PIFSC-27, Honolulu, HI.

Braun R., J. Wester, C., Mcdonald, and J. H., Pate. 2024. Perceptions regarding the recreational cobia fishery in relation to manta ray conservation. Aquatic Conservervation: Marine and Freshwater Ecosystms. https://doi.org/10.1002/aqc.4147

Braun, C. D., G. B. Skomal, S. R. Thorrold, and M. L. Berumen. 2015. Movements of the reef manta ray (Manta alfredi) in the Red Sea using satellite and acoustic telemetry. Marine Biology 162(12):2351-2362.

Burgess, K. B., and coauthors. 2016. Manta birostris, predator of the deep? Insight into the diet of the giant manta ray through stable isotope analysis. Royal Society Open Science 3(11):160717.

Booda, L. 1984. Manta ray wings, shark meat posing as scallops. Sea Technology 25(11): 7.

Chassot, E., M. Amandè, C. Pierre, R. Pianet, and R. Dédo. 2008. Some preliminary results on tuna discards and bycatch in the French purse seine fishery of the eastern Atlantic Ocean. Collective Volume Of Scientific Papers 64.

Carpentier, A.S., Berthe, C., Ender, I., Jaine, F.R., Mourier, J., Stevens, G., De Rosemont, M. and Clua, E., 2019. Preliminary insights into the population characteristics and distribution of reef (Mobula alfredi) and oceanic (M. birostris) manta rays in French Polynesia. Coral Reefs, 38(6), pp.1197-1210.

Chin, A., P. Kyne, T. Walker, and R. McAuley. 2010. An integrated risk assessment for climate change: Analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. Global Change Biology 16:1936-1953.

CITES. 2013. Consideration of proposals for amendment of Appendices I and II: Manta Rays. Convention on International Trace in Endangered Species of Wild Fauna and Flora (CITES), Sixteenth Meeting of the Conference of the Parties, CoP16 Prop. 46 (Rev. 2), Bangkok, Thailand.

Clark, T. B. 2010. Abundance, home range, and movement patterns of manta rays (Manta alfredi, M. birostris) in Hawai'i. Dissertation. Univeristy of Hawai'i at Mānoa, Honolulu, HI.

Cole, M., Lindeque, P., Fileman, E., Halsband, C., Goodhead, R., Moger, J., et al., (2013). Microplastic ingestion by zooplankton. Environ. Sci. Technol. 47, 6646–6655. doi: 10.1021/es400663f

Coles, R. J. 1916. Natural history notes on the devil-fish, Manta birostris (Walbaum) and Mobula olfersi (Muller). Bulletin of the American Museum of Natural History 35(33):649-657.

Convention on Migratory Species. 2014. Proposal for the inclusion of the reef manta ray (Manta alfredi) in CMS Appendix I and II. Convention on Migratory Species (CMS), 18th Meeting of the Scientic Council, UNEP/CMS/ScC18/Doc.7.2.9, Bonn, Germany.

Couturier, L. I. E., and coauthors. 2012. Biology, ecology and conservation of the Mobulidae. Journal of Fish Biology 80(5):1075-1119.

Couturier, L. I. E., and coauthors. 2013. Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. PLOS ONE 8(10):e77152.

Deakos, M. H. 2010. Ecology and social behavior of a resident manta ray (Manta alfredi) population of Maui, Hawai'i. Dissertation. Univeristy of Hawai'i at Mānoa, Honolulu, HI.

Deakos, M. H., J. D. Baker, and L. Bejder. 2011. Characteristics of a manta ray Manta alfredi population off Maui, Hawaii, and implications for management. Marine Ecology Progress Series 429:245-260.

Dewar, H., and coauthors. 2008. Movements and site fidelity of the giant manta ray, Manta birostris, in the Komodo Marine Park, Indonesia. Marine Biology 155(2):121-133.

Duffy, L. and Griffiths, S. 2017. Resolving potential redundancy of productivity attributes to improve ecological risk assessments. SAC-08-07c. Inter-American Tropical Tuna Commission. Scientific Advisory Committee Eight Meeting, La Jolla, California (USA), 8-12 May 2017.

Dulvy, N. K., S. A. Pardo, C. A. Simpfendorfer, and J. K. Carlson. 2014. Diagnosing the dangerous demography of manta rays using life history theory. PeerJ Preprints 2.

Essumang, D.K. 2010. First determination of the levels of platinum group metals in Manta birostris (manta ray) caught along the Ghanaian coastline. Bulletin of Environmental Contamination and Toxicology 84: 720-725.

Farmer, N.A., Garrison, L.P., 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

Fernando, D. and Stevens, G. 2011. A study of Sri Lanka's Manta & Mobula Ray Fishery. Manta Trust.

Fossi, M. C., Baini, M., Panti, C., Galli, M., Jiménez, B., Muñoz-Arnanz, J., et al., (2017). Are whale sharks exposed to persistent organic pollutants and plastic pollution in the Gulf of California (Mexico)? first ecotoxicological investigation using skin biopsies. Comp. Biochem. Physiol. C Toxicol. Pharmacol. 199, 48–58. doi: 10.1016/j.cbpc.2017.03.002

Fossi, M. C., Marsili, L., Baini, M., Giannetti, M., Coppola, D., Guerranti, C., et al., (2016). Fin whales and microplastics: the Mediterranean Sea and the Sea of Cortez scenarios. Environ. Pollut. 209, 68–78. doi: 10.1016/j.envpol.2015.11.02

Fossi, M. C., Coppola, D., Baini, M., Giannetti, M., Guerranti, C., Marsili, L., et al., (2014). Large filter feeding marine organisms as indicators of microplastic in the pelagic environment: the case studies of the Mediterranean basking shark (Cetorhinus maximus) and fin whale (Balaenoptera physalus). Mar. Environ. Res. 100, 17–24. doi: 10.1016/j.marenvres.2014.02.002

Francis, M.P. and Jones, E.G. 2017. Movement, depth distribution and survival of spinetail devilrays (Mobula japanica) tagged and released from purse-seine catches in New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 27(1): 219-236.

Frankham, R., Bradshaw, C. J., & Brook, B. W. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. Biological Conservation, 170, 56-63.

Galloway, T. S., and Lewis, C. N. (2016). Marine microplastics spell big problems for future generations. Proc. Nat. Acad. Sci. U.S.A. 113, 2331–2333. doi: 10.1073/pnas.1600715113

Germanov, E. S., Marshall, A. D., Bejder, L., Fossi, M. C., and Loneragan, N. R. (2018). Microplastics: no small problem for filter-feeding megafauna. Trends Ecol Evol. 33, 227–232. doi: 10.1016/j.tree.2018.01.005

Germanov, E. S., and A. D. Marshall. 2014. Running the gauntlet: regional movement patterns of Manta alfredi through a complex of parks and fisheries. PLOS ONE 9(10):e110071.

Germanov, E. S., and coauthors. 2019. Microplastics on the menu: Plastics pollute Indonesian manta ray and whale shark feeding grounds. Frontiers in Marine Science 6(679).

Girondot, M., and coauthors. 2015. Spatio-temporal distribution of Manta birostris in French Guiana waters. Journal of the Marine Biological Association of the United Kingdom 95(1):153-160.

Graham, N. A. J., and coauthors. 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. PLOS ONE 3(8):e3039.

Graham, R. T., and coauthors. 2012. Satellite tracking of manta rays highlights challenges to their conservation. PLOS ONE 7(5).

Gudger, E. W. 1922. The most northerly record of the capture in Atlantic waters of the United States of the giant ray, Manta birostris. Science 55(1422):338-340.

Guinder, V. A., and J. C. Molinero. 2013. Climate change effects on marine phytoplankton. Pages 68-90 in A. H. Arias, and M. C. Menendez, editors. Marine Ecology in a Changing World. CRC Press, Boca Raton, FL.

Handwerk, B. 2010, October 16. Little-known Gulf Rays Affected by Oil Spill?. National Geographic News. https://www.nationalgeographic.com/animals/article/101015-new-manta-rays-gulf-bp-oil-spill-science-animals.

Harty K, Guerrero M, Knochel AM, Stevens GMW, Marshall A, Burgess K, Stewart JD. 2022. Demographics and dynamics of the world's largest known population of oceanic manta rays Mobula birostris in coastal Ecuador. Mar Ecol Prog Ser 700:145-159. https://doi.org/10.3354/meps14189

Hearn, A. R., and coauthors. 2014. Elasmobranchs of the Galapagos Marine Reserve. Pages 23-59 in J. Denkinger, and L. Vinueza, editors. Social and Ecological Interactions in the Galapagos Island, The Galapagos Marine Reserve: A dynamic social-ecological system. Springer, New York, NY.

Heinrichs, S., M. O'Malley, H. Medd, and P. Hilton. 2011. Global Threat to Manta and Mobula Rays. Manta Ray of Hope, 2011 Report.

Heron, S. F., C. M. Eakin, J. A. Maynard, and R. van Hooidonk. 2016. Impacts and effects of ocean warming on coral reefs. Pages 177-197 in D. Laffoley, and J. M. Baxter, editors. Explaining Ocean Warming: Causes, scale, effects and consequences. IUCN, Gland, Switzerland.

Hilbourne S, Stevens G. 2019. Maldivian Manta Ray Project oceanic manta ray summary report 2019. The Manta Trust. https: //static1.squarespace.com/static/ 5a196500914e6b09132e911f/t/5d1090a94951180001880 a1d/1561366735894/MT_MMRP_Oceanic+Manta+ Summary+Report_2019_FINAL.pdf

Hinojosa-Alvarez S., Walter R.P., Diaz-Jaimes P., Galván-Magaña F. and Paig-Tran E.M. 2016. A potential third Manta Ray species near the Yucatán Peninsula? Evidence for a recently diverged and novel genetic Manta group from the Gulf of Mexico. PeerJ 4: e2586.

Holmberg Pierce, S.J. and Marshall, A.D., 2018. Photographic identification of sharks. Shark research: emerging technologies and applications for the field and laboratory, pp.219-234.

Hosegood, P.J., Nimmo-Smith, W.A.M., Proud, R., Adams, K. and Brierley, A.S., 2019. Internal lee waves and baroclinic bores over a tropical seamount shark 'hot-spot'. Progress in Oceanography, 172, pp.34-50.

Intergovernmental Panel on Climate Change. 2013. Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Cambridge, United Kingdom; New York, NY.

Jakimska, A., Konieczka, P., Skóra, K., and Namieśnik, J. 2011. Bioaccumulation of metals in tissues of marine animals, part I: the role and impact of heavy metals on organism. Pol. J. Enviro. Studies 20, 1127–1146.

Jambeck, J. R., and coauthors. 2015. Plastic waste inputs from land into the ocean. Science 347(6223):768-771.

Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci U S A 101(21):8251-8253.

Kashiwagi, T., T. Ito, and F. Sato. 2010. Occurences of reef manta ray, Manta alfredi, and giant manta ray, M. birostris, in Japan, examined by photographic records. Japanese Society for Elasmobranch Studies 46:20-27.

Kashiwagi, T., A. D. Marshall, M. B. Bennett, and J. R. Ovenden. 2011. Habitat segregation and mosaic sympatry of the two species of manta ray in the Indian and Pacific Oceans: Manta alfredi and M. birostris. Marine Biodiversity Records 4:1-8.

Knochel, A.M., Cochran, J.E., Kattan, A., Stevens, G.M., Bojanowksi, E. and Berumen, M.L., 2022. Crowdsourced data reveal multinational connectivity, population demographics, and possible nursery ground of endangered oceanic manta rays in the Red Sea. Aquatic Conservation: Marine and Freshwater Ecosystems, 32(11), pp.1774-1786.

Lawson, J. M., and coauthors. 2017. Sympathy for the devil: a conservation strategy for devil and manta rays. PeerJ 5:e3027.

Lawson, J. M., and coauthors. 2016. Sympathy for the devil: A conservation strategy for devil and manta rays. PeerJ 5:e3027.

Lewis, S.A., Setiasih, N., Dharmadi, Fahmi, O'Malley, M.P., Campbell, S.J., Yusuf, M. and Sianipar, A. 2015. Assessing Indonesian Manta and Devil Ray Populations Through Historical Landings and Fishing Community Interviews. PeerJ Preprints: available online at https://peerj.com/preprints/1334

Manta Trust. 2019a. Mooring Line Entanglement Mitigation. Manta Trust. Available online at: https://static1.squarespace.com/static/5a196500914e6b09132e911f/t/5dfe1e20b02a616945eb5772/1576934948296/MT_MMRP_Entanglement+Mitigation_2019_FINAL.pdf (accessed January 20, 2021).

Manta Trust. 2019b. Manta Ray Entanglement Protocol. Manta Trust. Available online at: https://static1.squarespace.com/static/5a196500914e6b09132e911f/t/5dfe2e70229b17607ddeb2c9/1576939123128/MT_MMRP_Entanglement+Protocol_2019_FINAL.pdf (accessed March 2, 2021).

MantaMatcher. 2016. Manta Matcher - The Wildbook for Manta Rays.

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Derrick, D., Herman, K., Jabado, R.W., Liu, K.M., Rigby, C.L. & Romanov, E. 2022. Mobula birostris (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2022: e.T198921A214397182. https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T198921A214397182.en

Marshall, A. D., L. J. V. Compagno, and M. B. Bennett. 2009. Redescription of the genus Manta with resurrection of Manta alfredi (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). Zootaxa 2301:1-28.

Medeiros, A. M., O. J. Luiz, and C. Domit. 2015. Occurrence and use of an estuarine habitat by giant manta ray Manta birostris. Journal of Fish Biology 86(6):1830-1838.

Milessi, A. C., and M. C. Oddone. 2003. Primer registro de Manta birostris (Donndorff 1798) (Batoidea: Mobulidae) en el Rio de La Plata, Uruguay. Gayana 67(1):126-129.

Miller, M. H., and C. Klimovich. 2017. Endangered Species Act status review report: Giant manta ray (Manta birostris) and reef manta ray (Manta alfredi). U.S. Department of Commerce, National Oceanic and Atmoshperic Administration, National Marine Fisheries Servcie, Office of Protected Resources, Silver Spring, MD.

Moazzam, M. 2018. Unprecedented decline in the catches of mobulids: an important component of tuna gillnet fisheries in the Northern Arabian Sea. IOTC-2018-WPEB14-30. Indian Ocean Tuna Commission Report.

Mogollón R, Calil PHR. 2018.Counterintuitive effects of global warming-induced wind patterns on primary production in the Northern Humboldt Current System. Glob Change Biol 24: 3187−3198

Moore, A. B. M. 2012. Records of poorly known batoid fishes from the north-western Indian Ocean (Chondrichthyes: Rhynchobatidae, Rhinobatidae, Dasyatidae, Mobulidae). African Journal of Marine Science 34(2):297-301.

Mourier, J. 2012. Manta rays in the Marquesas Islands: First records of Manta birostris in French Polynesia and most easterly location of Manta alfredi in the Pacific Ocean, with notes on their distribution. Journal of Fish Biology 81(6):2053-2058.

Nair, R.J., Zacharia, P.U., Kishor, T.G., Dinesh, K.S., Dhaneesh, K.V., Suraj, K.S., Siva, G.K. and Seetha, P.K. 2013. Heavy landings of mobulids reported at Cochin Fisheries Harbour, Kerala. Marine Fisheries Information Services, T&E Series 21: 19-20.

Nawaz, R. and Khan, M.M. 2015. Developing conservation strategy for Mobulids found in waters of Pakistan, 2013-2015. Final Project Report 2013-2015. WWF Pakistan and Save Our Seas Foundation, Pakistan.

NMFS (2020) Endangered Species Act Section 7 Biological Opinion on the Pelagic Longline Fishery for Atlantic Highly Migratory Species. F/SER/2014/00006[13697]

NMFS (2021) Endangered Species Act Section 7 Biological Opinion on the Reinitiation of Endangered Species Act Section 7 Consultation on the Implementation of the Sea Turtle Conservation Regulations under the ESA and the Authorization of the Southeast U.S. Shrimp Fisheries in Federal Waters under the Magnuson-Stevens Fishery Management and Conservation Act. SERO-2021-00087

NMFS (2023) Endangered Species Act Section 7 Biological Opinion on the Amendment to the 2015 Biological Opinion on the operation of the Coastal Migratory Pelagic Fishery as Managed by the Fishery Management Plan for Coastal Migratory Pelagic Resources in the Gulf of Mexico and Atlantic Region under the Magnuson-Stevens Fishery Conservation and Management Act. SERO-2021-03456.

NMFS. 2024. Endangered Species Act recovery status review for giant manta rays (mobula birostris). U.S. Department of Commerce, National Oceanic and Atmospheric Adminstartion, National Marine Fisheries Service, Office of Protected Resources, Silver Springs MD.

Notarbartolo di Sciara, G., and E. V. Hillyer. 1989. Mobulid rays off eastern Venezuela (Chondrichthyes, Mobulidae). Copeia (3):607-614.

O'Malley, M. P., K. Lee-Brooks, and H. B. Medd. 2013. The global economic impact of manta ray watching tourism. PLOS ONE 8(5):e65051.

Oliver, S., M. Braccini, S. J. Newman, and E. S. Harvey. 2015. Global patterns in the bycatch of sharks and rays. Marine Policy 54:86-97.

Ooi, M.S.M., Townsend, K.A., Bennett, M.B., Richardson, A.J., Fernando, D., Villa, C.A. and Gaus, C. 2015. Levels of arsenic, cadmium, lead and mercury in the branchial plate and muscle tissue of mobulid rays. Marine Pollution Bulletin 94(1): 251-259.

Oyarzún D, Brierley CM.2018. The future of coastal up - welling in the Humboldt Current from model projections. Clim Dyn 52: 599−615

Pate, J. Evidence of reproductive and feeding habitat for manta rays off Florida’s Atlantic coast. Environ Biol Fish (2024). https://doi.org/10.1007/s10641-024-01566-7

Pate, J. H., and Marshall, A. D. 2020. Urban manta rays: potential manta ray nursery habitat along a highly developed Florida coastline. Endanger. Species Res. 43, 51–64. doi: 10.3354/esr01054

Pate J.H, Macdonald C., Wester J. 2020. Surveys of recreational anglers reveal knowledge gaps and positive attitudes towards manta ray conservation in Florida. Aquatic Conservation Marine and Freshwater Ecosystems. 31. 10.1002/aqc.3508.

Raje, S.G., Sivakami, S., Mohanraj, G., Manojkumar, P.P., Raju, A. and Joshi, K.K. 2007. An atlas on the Elasmobranch fishery resources of India. CMFRI Special Publication, 95. 1-253.

Rambahiniarison, J. M., and coauthors. 2018. Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea, Philippines. Frontiers in Marine Science 5:269.

Roberts, B. 2022. Catch Cobia on migrating manta rays: cobia can't resist hanging around these giant rays on the move this month. Florida Sportsman. First published Florida Sportsman April 2015. https://www.floridasportsman.com/editorial/cobia-rays/400722

Romanov, E. V. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. Fishery Bulletin 100(1):90-105.

Rohner, C.A., Flam, A.L., Pierce, S.J. and Marshall, A.D. 2017. Steep declines in sightings of manta rays and devilrays (Mobulidae) in southern Mozambique. PeerJ Preprints 5: e3051v1.

Rohner, C. A., Weeks, S. J., Richardson, A. J., Pierce, S. J., Magno-Canto, M. M., Feldman, G. C., et al., (2014). Oceanographic influences on a global whale shark hotspot in southern Mozambique. PeerJ PrePrints. 2:e661v1. doi: 10.7287/peerj.preprints.661v1

Rochman, C. M., Kurobe, T., Flores, I., and Teh, S. J. (2014). Early warning signs of endocrine disruption in adult fish from the ingestion of polyethylene with and without sorbed chemical pollutants from the marine environment. Sci. Total Environ. 493, 656–661. doi: 10.1016/j.scitotenv.2014.06.051

Rubin, R. D., K. R. Kumli, and G. Chilcott. 2008. Dive characteristics and movement patterns of acoustic and satellite-tagged manta rays (Manta birostris) in the Revillagigedos Islands of Mexico. American Elasmobranch Society, Montreal, Canada.

Rubin, R. 2002. Manta rays: not all black and white. Shark Focus 15: 4-5.

Setälä, O., Fleming-Lehtinen, V., and Lehtiniemi, M. 2014. Ingestion and transfer of microplastics in the planktonic food web. Environ. Pollut. 185, 77–83. doi: 10.1016/j.envpol.2013.10.013

Stewart, J. D., E. M. Hoyos-Padilla, K. R. Kumli, and R. D. Rubin. 2016. Deep-water feeding and behavioral plasticity in Manta birostris revealed by archival tags and submersible observations. Zoology 119.

Stewart, J. D., M. Nuttall, E. L. Hickerson, and M. A. Johnston. 2018. Important juvenile manta ray habitat at Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico. Marine Biology 165:111.

Stewart, J.D., Jaine, F.R.A., Armstrong, A.J., Armstrong, A.O., Bennett, M.B., Burgess, K.B., Couturier, L.I.E., Croll, D.A., Cronin, M.R., Deakos, M.H., Dudgeon, C.L., Fernando, D., Froman, N., Germanov, E.S., Hall, M.A., Hinojosa-Alvarez, S., Hosegood, J.E., Kashiwagi, T., Laglbauer, B.J.L., Lezama-Ochoa, N., Marshall, A.D., McGregor, F., Notarbartolo di Sciara, G., Palacios, M.D., Peel, L.R., Richardson, A.J., Rubin, R.D., Townsend, K.A., Venables, S.K. and Stevens, G.M.W. 2018. Research priorities to support effective manta and devil ray conservation. Frontiers in Marine Science 5(314).

Stewart, J. D., Barroso, A., Butler, R. H., and Munns, R. J. 2018b. Caught at the surface: myctophids make easy prey for dolphins and devil rays. Ecology. 99, 1894–1896. doi: 10.1002/ecy.2348

Stewart, J. D., Nuttall, M., Hickerson, E. L., and Johnston, M. A. 2018c. Important juvenile manta ray habitat at flower garden banks national marine sanctuary in the northwestern Gulf of Mexico. Mar. Biol. 165:111. doi: 10.1007/s00227-018-3364-5

Stewart, J. D., Beale, C. S., Fernando, D., Sianipar, A. B., Burton, R. S., Semmens, B. X., et al., (2016a). Spatial ecology and conservation of manta birostris in the indo-pacific. Biol. Conserv. 200, 178–183. doi: 10.1016/j.biocon.2016.05.016

Stewart, J. D., Hoyos-Padilla, E. M., Kumli, K. R., and Rubin, R. D. 2016b. Deep-water feeding and behavioral plasticity in Manta birostris revealed by archival tags and submersible observations. Zoology 119, 406–413. doi: 10.1016/j.zool.2016.05.010.

Sussarellu, R., Suquet, M., Thomas, Y., Lambert, C., Fabioux, C., Pernet, M. E., et al., 2016. Oyster reproduction is affected by exposure to polystyrene microplastics. Proc. Nat. Acad. Sci. U.S.A. 113, 2430–2435. doi: 10.1073/pnas.1519019113

Tremblay-Boyer, L. and Brouwer, S. 2016. Review of information on non-key shark species including mobulids and fisheries interactions. EB-WP-08. Western Central Pacific Fisheries Commission. Scientific Committee Twelfth Regular Session. Bali, Indonesia 3–11 August 2016.

Venables, S. 2013. Short term behavioural responses of manta rays, Manta alfredi, to tourism interactions in Coral Bay, Western Australia. Thesis. Murdoch University.

White, E.R., Myers, M.C., Flemming, J.M. and Baum, J.K. 2015. Shifting elasmobranch community assemblage at Cocos Island--an isolated marine protected area. Conservation Biology 29(4): 1186–1197

Ward-Paige, C.A., David, B. and Worm, B. 2013. Global population trends and human use patterns of Manta and Mobula rays. PLoS ONE 8(9): e74835. doi:10.1371/journal.pone.0074835.