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Mobulid Rays off Eastern Venezuela (Chondrichthyes, Mobulidae)

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Aerial surveys in the Venezuelan Caribbean Sea between Puerto la Cruz and Isla Margarita documented the presence, distribution, color patterns and habits of two mobulid rays, *Manta birostris* and *Mobula tarapacana*. *Manta birostris* was regularly observed; *Mobula hypostoma*, the only *Mobula* known from the Caribbean Sea, was never seen. By contrast, *M. tarapacana*, a circumtropical mobulid previously unreported from the Caribbean Sea, was occasionally sighted. *Manta birostris* was observed between March and Dec., mainly in shallow waters in two preferred locations of the study area; numbers were greatest in the fall. Conversely, *Mobula tarapacana* was seen mainly in deep waters between April and Nov. The area appears to be a major feeding ground for *Manta birostris* in the Caribbean. Although schooling was not seen, mantas were occasionally found in aggregations of up to 50 individuals. Most sightings of *Mobula tarapacana* were of solitary individuals; schooling was observed once.

THIS study documents the presence, seasonal abundance, distribution, and habits of mobulid rays found in the Venezuelan Caribbean Sea. Habits and ecology of these highly specialized, pelagic elasmobranchs are practically unknown, and no long-term investigations of their natural history have been published.

Two mobulid species, *Manta birostris* (Donndorff, 1798) and *Mobula hypostoma* (Bancroft, 1831) are known from the Caribbean Sea (Bigelow and Schroeder, 1953). *Manta birostris*, commonly known as "manta," "manta ray," or "devil ray," is the largest batoid and one of the largest elasmobranchs, reaching a disc width of

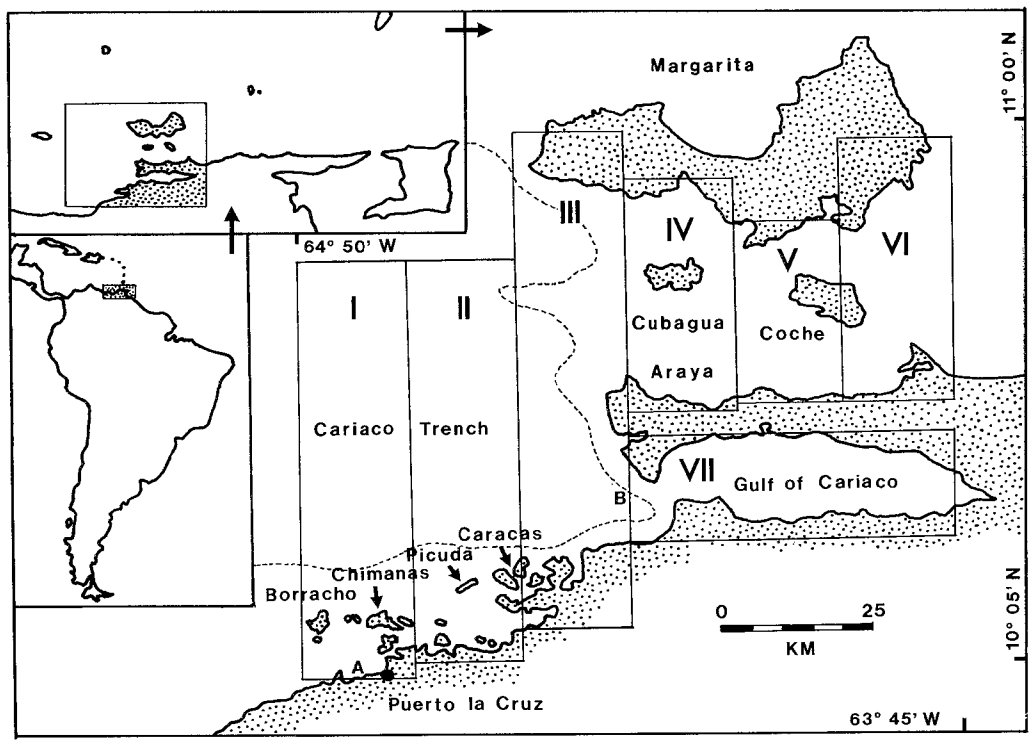

Fig. 1. The study area with the survey strips (numbered I–VII). The dotted line is the 200 m depth contour. A, B: survey starting or ending points, respectively, near Puerto la Cruz and at the entrance of the Gulf of Cariaco, Venezuelan Caribbean Sea.

at least 6.7 m and a weight of more than 1360 kg (Bigelow and Schroeder, 1953). *Manta birostris* is circumtropical; its presence in Venezuelan waters is well documented (Bancroft, 1829; Schultz, 1949; Gines, 1972). *Mobula hypostoma*, a small, often gregarious species, reaching a maximum disc width of 1.2 m, is the only species of *Mobula* known from the tropical western Atlantic, ranging from the United States south to Argentina (Notarbartolo di Sciara, 1987). Reports of *M. hypostoma* from the Caribbean abound, and are summarized by Bigelow and Schroeder (1953). Those authors, however, speculated that other large *Mobula* species may occur in the western Atlantic, including *M. mobular* (Bonnaterre, 1788), the only other *Mobula* known from the Atlantic Ocean at that time.

The impetus for the present study was provided by collisions in 1977 and 1978 off eastern Venezuela between passenger-carrying hydrofoils and large marine vertebrates of undetermined species. Reconnaissance surveys verified that cetaceans and large elasmobranchs did occur in that region and established the need for detailed research to determine whether high-speed passenger vessels could operate there safely. Between Oct. 1978 and Nov. 1979 low-altitude aerial surveys examined occurrence, distribution, seasonal abundance, behavior and other aspects of the biology of large marine vertebrates, including mobulid rays, in the waters adjacent to Puerto la Cruz and Isla Margarita. Surface cruises to examine animals at close quarters supplemented aerial observations. *Manta birostris* was regularly observed; *Mobula hypostoma* was never seen. By contrast, *M. tarapacana* (Philippi, 1892), a circumtropical mobulid previously unreported from the Caribbean Sea, was occasionally sighted.

Methods

The study area, located between 10°05'N–11°00'N and 63°45'W–64°50'W (total water surface 5800 km²), was divided into seven rectangular strips, 18.5 km (10 nautical miles [nm])

TABLE 1. SUMMARY OF SIGHTINGS OF *Manta birostris* AND *Mobula tarapacana*. The numbers in parentheses represent the number of individuals sighted. "Other methods" include sightings from the aircraft during reconnaissance flights and connecting legs between transects, and sightings from the boat. Data on *M. tarapacana* are pooled because of the small sample size.

Month	*Manta birostris*			*Mobula tarapacana*
	Aerial survey	Other methods	Total	All methods
January	0	0	0	0
February	0	0	0	0
March	0	4 (11)	4 (11)	0
April	7 (8)	21 (44)	28 (52)	1 (1)
May	8 (10)	21 (90)	29 (100)	2 (3)
June	5 (5)	3 (6)	8 (11)	1 (1)
July	2 (2)	1 (1)	3 (3)	5 (13)
August	3 (37)	7 (7)	10 (44)	4 (4)
September	4 (50)	5 (15)	9 (65)	1 (1)
October	1 (3)	0	1 (3)	2 (4)
November	2 (2)	1 (1)	3 (3)	5 (5)
December	1 (1)	2 (2)	3 (3)	0
Total	33 (118)	65 (177)	98 (295)	21 (32)

wide but variable in length. Six strips (I–VI) were oriented north–south; the seventh, over the Gulf of Cariaco, was oriented east–west (Fig. 1). Each aerial survey consisted of seven transects flown lengthwise within each strip, and the necessary connecting legs between adjacent strips (average survey length 323 km over water). Surveys alternately began from Puerto la Cruz or from the entrance to the Gulf of Cariaco (respectively A and B, Fig. 1), with consequent alternation of transect direction within each strip. For transect selection, north and south boundaries of strips I–VI and east and west boundaries of strip VII were marked off at 0.93 km (0.5 nm) intervals and numbered 1–20. For each survey, two numbers were selected at random for each zone to serve as transect starting and ending points; these points were connected to assign aircraft headings.

The study area was surveyed 38 times. Between Oct. 1978 and Jan. 1979 observations were made from a "Piper Cherokee"; all subsequent surveys were conducted from "Cessnas." To record and photograph behaviors and color patterns, 13 additional flights were made over the areas in which animals were known to be most abundant and on the waters surrounding the study area (between Islas Tortuga, La Blanquilla, and Testigos). Overall flight time was 188 h.

In addition to the pilot there were one (seven flights), two (30 flights), or three or more (14 flights) observers on board; the principal observer was in the right front seat. One of us (GNdS) participated in all flights. The airplane flew at an average altitude of 230 m and an average ground speed of 165 km/h. No surveys were conducted when sea state was visually estimated at Beaufort 4 or greater (Leatherwood et al., 1978); such conditions occurred only twice (in Feb.), causing suspension of surveys with only a partial set of data. Flights were made early in the morning, when the sea was generally calm.

Mobulid rays were easily recognizable among surface-dwelling myliobatiforms because of greater body size and prominent cephalic fins. Dorsal coloration and size of head relative to disc width permitted distinction of *Mobula* from *Manta*.

Sailing vessels, used to approach and observe cetaceans at close quarters, also afforded observation of mobulids. Breaching mantas were particularly visible from surface craft. Vessel observations, however, could only indicate occurrence of rays in particular locations, as boat effort was not quantified.

RESULTS

Manta birostris was sighted 98 times; a total of 295 individuals were counted. Of all rays sighted, 40% (118) were seen during the survey; the rest were seen both from the air during connecting legs between adjacent transects or when

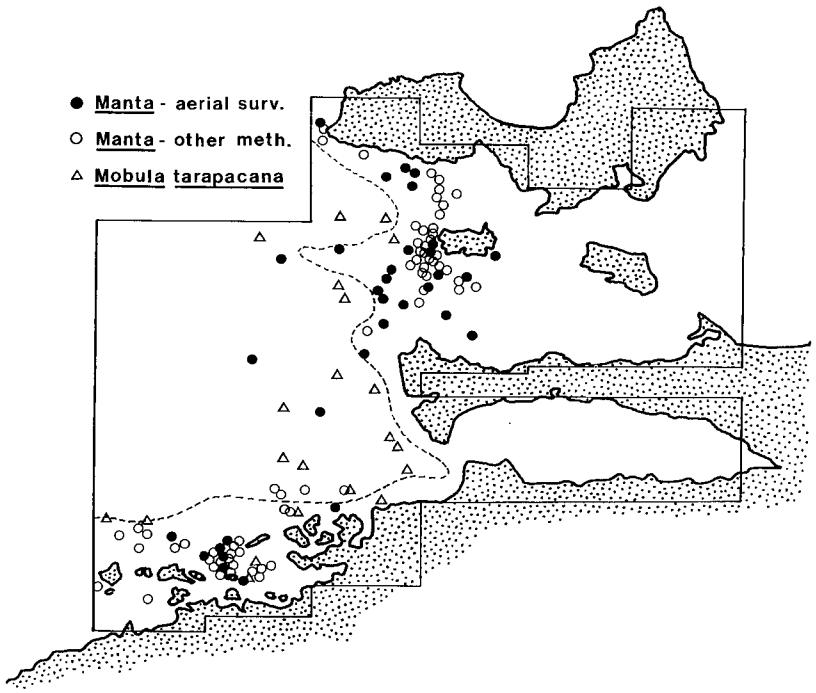

Fig. 2. Locations of sightings of *Manta birostris* and *Mobula tarapacana* in the Venezuelan Caribbean Sea (for more detail, see Fig. 1).

flying over the waters surrounding the study area, and from sailing vessels. *Mobula tarapacana* was observed 21 times; a total of 32 individuals were counted (Table 1). Most *M. tarapacana* (88%) were seen from the air.

Locations of sightings of *Manta birostris,* both from the air and the surface, are shown in Figure 2. The presence of rays was very predictable in two preferred locations: a narrow area located between Isla Margarita, the Araya peninsula, Isla Cubagua and the 200 m depth contour; and the region between the small islands facing Puerto la Cruz (Cayo Borracho, Islas Chimanas, Picudas and Caracas) and the 200 m depth contour. A few rays were seen in the waters surrounding the study area, over the continental shelf north of Isla Margarita (April and May), and in the vicinity of Isla Tortuga. Contrary to expectations, mantas were never seen east of Cubagua in the shallow waters between Isla Margarita and the mainland, nor in the Gulf of Cariaco. The distribution of mantas within the study area was constant throughout the year. Rays showed a distinct preference for neritic waters and were often less than 50 m from shore. By contrast, only seven individuals (2.4%) were seen swimming over the deep waters of the Cariaco Trench.

The seasonal abundance of *M. birostris* at or near the surface is presented in Table 2. No ray was seen in Jan. or Feb. The mantas increased

TABLE 2. SEASONAL ABUNDANCE OF *Manta birostris.* N = number of surveys conducted in each period; $\bar{x}$ = mean number of rays sighted per survey; SD = standard deviation; SE = standard error of the mean.

	N	$\bar{x}$	2SE	SD
Jan.–Feb.	2	0	0	0
March–April	8	1.0	1.7	2.4
May–June	8	1.9	1.3	1.8
July–Aug.	8	4.9	8.6	12.2
Sept.–Oct.	4	13.3	12.6	12.6
Nov.–Dec.	8	0.4	0.4	0.5

TABLE 3. SEASONAL VARIATION OF THE FREQUENCIES OF COLOR PATTERNS OF THE DORSAL SIDE OF *Manta birostris*.

	Nov.–April		May–Oct.		Total	
	n	%	n	%	n	%
Black with white marks	24	57.1	24	64.9	48	60.8
Black without marks	7	16.7	13	35.1	20	25.3
Reddish-brown	11	26.2	0	0	11	13.9
Total	42	100	37	100	79	100

progressively between spring and early summer, peaked in Sept.–Oct. and dropped abruptly towards the end of the year. This coincided with the opinion of the fishermen we interviewed, who maintained that mantas are most abundant towards the end of the rainy season. The moderate size of the sample may account for the large standard errors. Most of the sightings (75% of the rays seen from the air) appeared to be single individuals. Schooling was never observed. In all instances in which two or more rays were sighted within a small distance from each other (i.e., less than approx. 10 disc widths), they appeared uncoordinated, simply as if attracted to the same location by a commonly-sought resource. Aggregations of 30 or more individuals (up to 50) were seen in May, Aug., and Sept. Differences between mean monthly group sizes, however, were insignificant.

The behavior of *M. birostris* varied with water depth. All rays sighted in pelagic waters (>200 m) were travelling at a sustained speed and swam in a straight line, their cephalic fins tightly curled up. Most mantas found over the continental shelf (88%) appeared instead to be either resting or swimming very slowly without a clear heading, their cephalic fins loose, and their wingtips often curled up and protruding from the sea surface. Mantas often breached; splashes from their repeated somersaults were the most frequent sighting cue during vessel observations.

Manta birostris was often close to other marine vertebrates. These included common dolphins (*Delphinus delphis*), birds (*Pelecanus occidentalis, Fregata magnificens, Sterna* spp.), and elasmobranchs (*Sphyrna* sp., *Carcharhinus* spp., *Aetobatus narinari*). The pigmentation of *M. birostris* shows great variability (Bigelow and Schroeder, 1953). Three dorsal color patterns were observed: black with white marks, plain black, and reddish-brown. The white patterns on the dark dorsal background consisted mainly of two symmetrical, triangular "shoulder patches" located on either side of the nuchal region. The patches were either immaculate, or with dark spots in the middle. Rarer coloration features included white tips on the pectoral fins (dorsally), and a medial white chevron mark, its apex pointed caudally and coinciding with the dorsal fin origin. Pattern brightness varied from pure white to faded gray, the latter barely visible. The frequency of the three observed color patterns varied with the season (Table 3). About 60% of the sightings consisted of mantas bearing white marks on their backs. By contrast, plain-colored rays were predominantly reddish-brown in winter, and entirely black in summer. All ventral sides seen (during breachings or inverted swimming) were white.

All *Mobula tarapacana* were 2–3 m wide (compared with the shadow of the aircraft), and had a light-brown dorsal coloration. Although specimens could never be examined closely, we identified them as *M. tarapacana* because it is the only *Mobula* species that fits the observed morphological characters (Notarbartolo di Sciara, 1987). This large, circumtropical *Mobula* has not been reported before from the tropical western Atlantic, but its presence there is predictable. Locations of sightings are shown in Figure 2. *Mobula tarapacana* was usually found farther offshore than *Manta birostris,* most often in blue pelagic waters deeper than 200 m, and never in the green, shallow waters between Isla Margarita and the mainland. *Mobula tarapacana* was less common than *Manta birostris.* It was sighted between April and Nov., with a slight predominance of sightings in July. All specimens were alone, with the notable exception of a group of nine rays observed in July, 45 km NE of Puerto la Cruz, which were swimming in a tight circular formation (Fig. 3). Such behavior has not been reported for myliobatiform

Fig. 3. A school of *Mobula tarapacana* swimming in a circular formation.

rays, and its ethological significance remains problematical.

Discussion

Systematics of the genus *Manta* are still unsettled. Some authors (Whitley, 1936; Beebe and Tee-Van, 1941; Barton, 1948) have suggested that *Manta* consists of several species, the divisions based mainly on coloration characters. However, coloration, as shown in the present study, can be a misleading taxonomic tool in this batoid. Our observations of large groups of *Manta*, all apparently identical except for their dorsal coloration, suggest intraspecific color variation. White markings are not a sexual character in *Manta*, since they are found in both sexes (Beebe and Tee-Van, 1941); nor are they a juvenile trait as in *Mobula japanica* and *M. mobular* (Notarbartolo di Sciara, 1987), as they were commonly observed in fully grown individuals. If *Manta*'s large size releases it from predation pressure, coloration may not be under the strict control of natural selection. The shape and brightness of the shoulder patches varied greatly; some patches had darker spots in their middle, some did not. This argues against Beebe and Tee-Van's (1941) proposal that Atlantic and Pacific *Manta* are different species, which was based solely on the presence (Atlantic) or absence (Pacific) of dark spots within the shoulder patches of the specimens they examined. The apparent seasonal color variation, suggested by the disappearance of reddish-brown mantas in summer, is difficult to understand, and needs closer investigation. Reddish-brown mantas have been reported previously (Bigelow and Schroeder, 1953), but season was not specified.

The study area is one of the most productive regions of the Caribbean Sea. The North Equatorial Current, which enters the Caribbean through the Lesser Antilles and flows westward along the Venezuelan coast, conveys nutrient-rich water from the mouths of the Orinoco and Amazon rivers (Gade, 1961). Furthermore, upwellings are reported in the waters surrounding Isla Margarita, probably caused by the Ekman transport induced by the tradewinds (Ljöen and Herrera, 1965). Such oceanographic features create the conditions for very high primary production, which reaches 1860 mg C/m^2/day in the Gulf of Cariaco (Gines, 1972). Thus the study area may be an important feeding ground for *Manta birostris*. During most of our observations mantas were seen moving about in various directions, their cephalic fins unfurled as if skimming the surface; these behaviors indicate feeding in mobulids. Their consistent, predictable presence in two limited regions within the area may be related to particular ecological needs of their preferred prey species. *Manta*'s

frequent association with other marine vertebrates has often been interpreted as a multispecies feeding aggregation on a common prey.

Our study confirmed the local fishermen's conviction that mobulid rays are rare in winter and abundant in summer and fall. This seems to be a widespread feature of northern hemisphere mobulids. Summer occurrence of *Manta* was reported by Coles (1915, 1916) off North Carolina, and by Vaillant and Diguet (1898) in the Gulf of California. Many *Mobula* species are also seen or caught more often in summer than in winter in the northern hemisphere: *Mobula japanica* in California (Radovich, 1961; Notarbartolo di Sciara, 1987); *M. thurstoni, M. japanica* and *M. tarapacana* in the Gulf of California (Notarbartolo di Sciara, 1988); *M. olfersi* (=*M. hypostoma*) off North Carolina (Coles, 1913); and *M. mobular* in the Italian Mediterranean (Notarbartolo di Sciara and Serena, 1988). Summer northbound migration may account for greater abundance of mobulids in the warmer months in temperate waters. By contrast, the summer increase of abundance of mobulids in many northern tropical seas is probably not caused by migration. We suspect that mobulids do not migrate northward in the summer in the northwestern Atlantic, as their summer increase in abundance is simultaneous both in tropical and warm temperate waters. More likely, during winter mobulids either disperse offshore, where frequency of sightings decreases, or move to deep waters.

Observing and counting wildlife from aircraft is a widely used method for the study of marine mammal populations (Hammond, 1986). Aerial survey methods were adopted for this study because large cetaceans (notably the Bryde's whale, *Balaenoptera edeni*) were the major threat to the hydrofoil operations, and because knowledge concerning the presence of mantas at the surface was of interest to the sponsor of the study. Unlike cetaceans, however, mantas seen at the surface are not necessarily a representative sample of the total population, since they are not linked to the surface by a constant need for atmospheric oxygen. By contrast, the reasons that bring them to the surface, and thus within view, are largely unknown. Thus the assumption that the distribution and seasonal abundance of *Manta birostris* as described here reflects the ecology of the entire population cannot be safely made; adding a third dimension to our observations could bring major modifications to the picture presented in this study. However, we hypothesize that the ecological features of *M. birostris* described here are not an artifact of the research method adopted; this remains to be confirmed by other methods of investigation.

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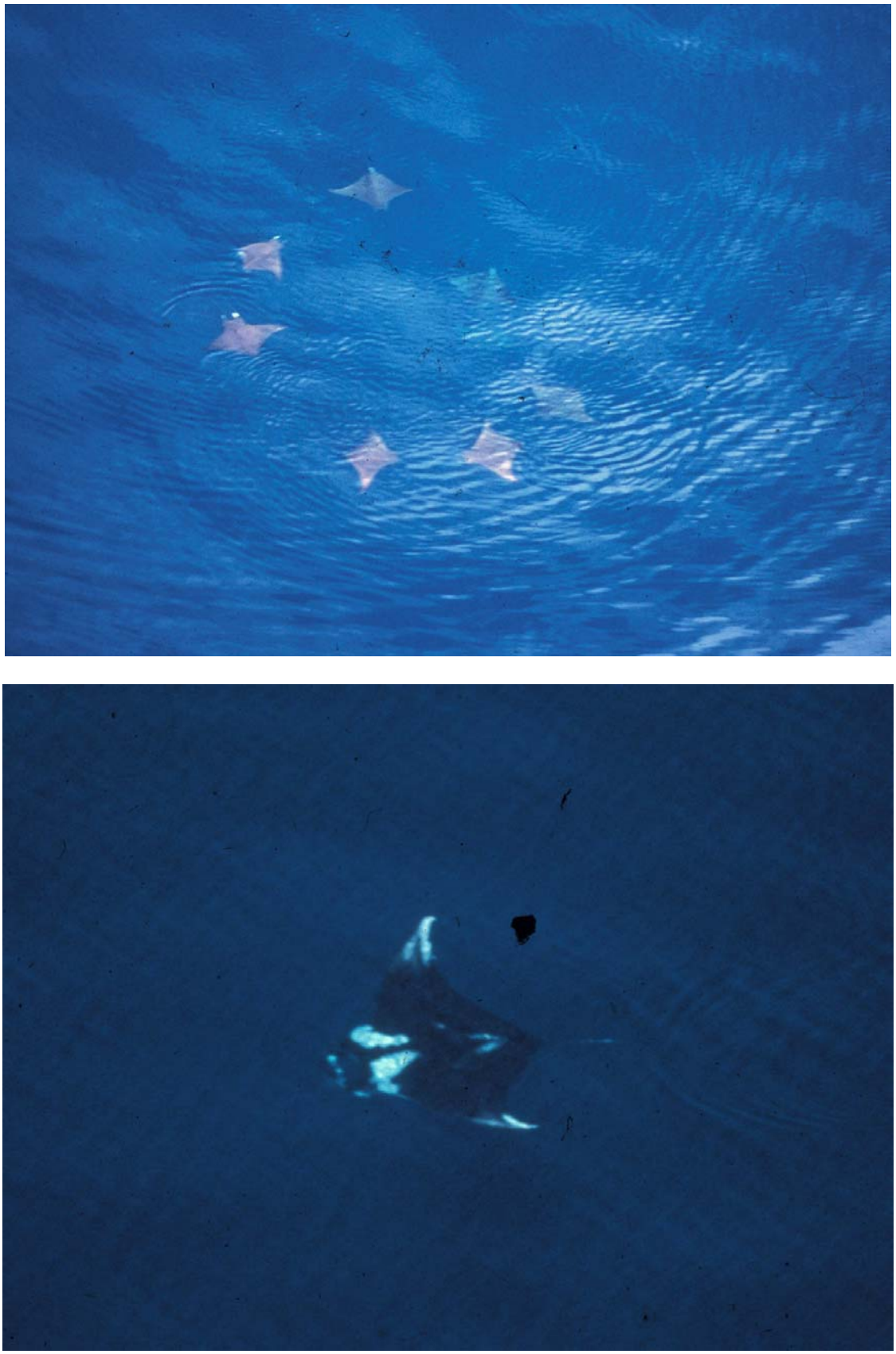

Aerial photographs of mobulid rays (top: *Mobula tarapacana*; bottom: *Manta birostris*) taken during surveys in Venezuela, 1978-79.